THE BRACHYOPID LABYRINTHODONTS

BY

DAVID MEREDITH SEARES WATSON, F.R.S.

Trustee of the British Museum

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By D. M. S. WATSON

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INTRODUCTION

The amphibia now known as "Labyrinthodonts" were first mentioned in print in G. F. Jaeger (1824 : 10), who, in 1828, published figures of three teeth called *Mastodonsaurus*, two "vertebrae" (which are intercentra), and a pair of exoccipitals held together by parasphenoid which he named "*Salamandroides giganteus*". Later he recognized that teeth and skull fragments were from the same animal, whose correct name was *Mastodonsaurus giganteus*.

In 1841 R. Owen obtained a tooth of *Mastodonsaurus* and showed (1842) that in section it had a dentine of unique complexity, found also in fragments of teeth from Warwick. He called both materials "*Labyrinthodon*". This generic name is an absolute synonym of *Mastodonsaurus*, but it may well be retained in the name of a group of higher rank.

During this decade Labyrinthodonts were described in considerable numbers from the Permian and Trias of Germany and Russia, and the next ten years added Canada, India, Australia and South Africa to their known distribution, and extended it downward to the Coal Measures. Thus by 1918 not only had a very large number of Labyrinthodonts been named, but other groups of Palaeozoic amphibia had been established, and a great number of new animals attributed to one or other of them. But the one hundred and twenty-three genera listed in the third edition of Zittel's *Grundzüge* by Broili were scattered amongst a number of major groups without real evidence, and nothing was known of the evolutionary history of any of them. The best summary was that by O. Abel in *Die Stämme der Wirbeltiere*, 1919.

In 1912 I gave a short account of some features of the skulls of two Labyrinthodonts from the Middle Coal Measures showing that the two, though clearly not closely related, agreed in many fundamental characters, including a single basioccipital condyle, reptile-like basipterygoid processes, pterygoids which so closely approach the middle line as to leave only slits as interpterygoid vacuities, and a narrow parasphenoid sheathing closely an interorbital septum. These qualities are largely those of *Seymouria*, and of Reptiles, but they are also found in the Osteolepid fish *Megalichthys*.

In 1919 I reviewed the Permian and Triassic Labyrinthodonts of the world and showed that they had vertebrae which had separate neural arches, pleurocentra and intercentra in Rhachitomi—the pleurocentra vanishing in certain late forms, the "Stereospondyli". However, the pattern of the dorsal surface of the skull, the lower jaw, clavicular arrangement, scapulo-coracoid, pelvis and proximal limb bones do not enable an animal to be referred to one or other group, though they are diagnostically Labyrinthodont.

Thus I was enabled to take the great mass of Labyrinthodonts of Permian and Triassic time together, and by comparing all known Lower Permian with all known Upper Triassic forms it became clear that the Labyrinthodonts display the following "advances":

(1) A gradual flattening of skull and body.

(2) A gradual reduction of the basioccipital and its retreat from the condyle.

(3) A reduction of the basipterygoid articulation and its functional replacement by a sutural attachment of an enlarged parasphenoid to the pterygoid.

(4) The exoccipitals extend to form the whole occipital condyle, reach forward to the pterygoids below the ear, and up to sutures with the new occipital flanges of the dermosupraoccipitals and tabulars.

(5) Reduction and final disappearance of cartilage bones in the paroccipitals, proötics, supraoccipital, as well as in the basisphenoid and basioccipital.

(6) An exaggeration of the interpterygoid vacuities and a reduction and shortening of the palatal ramus of the pterygoid.

(7) A reduction of the suspensory part of the skull so that the quadrate condyles come to lie in front of the occipital condyle.

Subsequently, in 1926, I was able to describe good material of several large Coal Measure Labyrinthodonts belonging to the two groups of Loxommids and Anthracosaurs. These animals, although they evidently differ a good deal from one another, agree in many features; they have a single nearly circular occipital condyle to which the small exoccipitals contribute; the supraoccipital is bony; there are no occipital flanges of the tabulars and dermosupraoccipitals; the basisphenoid has small basipterygoid processes, with articular faces for the pterygoid (and epipterygoid); the parasphenoid has a narrow ramus cultriformis sheathing the lower edge of an interorbital septum; the pterygoids meet one another in front, and leave only narrow slits as interpterygoid vacuities; the quadrate condyles lie far behind the occiput. In fact in all these respects they represent a logical starting point for the series of evolutionary changes deduced from observation of the then known later Labyrinthodonts. And they evidently make a real approach to the structure found in Osteolepid fishes.

At that time it seemed obvious that further progress required the adequate description of many other Labyrinthodonts, often named but not giving evidence about matters of importance. Dr. M. C. Steen therefore began a study of the faunas of fossil amphibia from the Coal Measures of Nýřany, Bohemia; Linton, Ohio; and the erect trees of South Joggins, Nova Scotia. In a series of papers 1931–1938 she revised these faunas, immensely increasing our real knowledge of them. Simultaneously A. S. Romer independently revised the Linton fauna, his results agreeing generally with those of Dr. Steen.

These re-examinations recognized in the Linton fauna a large number of animals with an incomprehensible vertebral column, which were referred to the Phyllospondyli, together with an obvious Loxommid, and *Leptophractus*, not yet adequately known. When in 1937 Dr. Steen examined the Lower Permian *Acanthostoma*, which is certainly a Labyrinthodont, she discovered that it possessed paired pleurocentra and intercentra, which were directly comparable to those of the Linton " Phyllospondyli ", and referred them to the Labyrinthodontia as " Rhachitomi ". Thus the rhachitomous stage of Labyrinthodont evolution was shown to have occurred in Coal Measure rocks in Europe and North America, but at a horizon clearly considerably higher than that of the Newsham and Scottish Coal Measure localities which produced Loxommids and Anthracosaurs. Finally Dr. Steen described a series of small closely related Labyrinthodonts from South Joggins of an age which is considerably older than that of the Linton and Nýřany faunas. It is, however, to be noted that *Eugyrinus wildi* (A. S. W.), which I held to be a Branchiosaur, is now regarded by Romer as a " Rhachitomous " Labyrinthodont. Its skull is in fact, though only 18 mm. in length, very much like that of the Dendrerpetons (cf. Text-figs. 29–31 of *Platystegos*). Indeed it is the only other form to show the peculiar arrangement whereby the squamosal is attached to the supratemporal by a special inwardly directed process. It has enlarged interpterygoid vacuities, relatively larger than those of *Dendrerpeton*, and is the oldest Labyrinthodont (or indeed amphibian) to show them. It has much cartilage bone and is presumably adult.

In 1931 G. Säve-Söderbergh, at the age of 21, collected from rocks in East Greenland, then held to be of Upper Devonian age and certainly containing fish of Old Red Sandstone type, a series of skulls of amphibia of entirely unknown type. He published a preliminary description of these fossils in 1932 and called them the Ichthyostegids. Further materials were collected in later years, but the prolonged illness and death of Säve-Söderbergh prevented any further preparation and description of them. At last in 1952, twenty years after the original description, Dr. Jarvik gave us an admirable account of the tail and hind limb of *Ichthyostega*, a set of new restorations of the skull of that animal, and a short account of a new, related, though very different animal—*Acanthostega*.

Thus it was clear that the whole group of Labyrinthodonts deserved re-examination. The general scheme of evolution I had described was based on gross comparisons of faunas of successive age, and it was obviously necessary to attempt to trace individual evolutionary lines through as long periods as possible, and in considerable detail. This I had begun, but was unable to complete, so that the appearance in 1947 of a great review of the Labyrinthodontia by Professor A. S. Romer was most valuable. Romer made no formal classification, nor did he attempt to isolate individual evolutionary lines, but he brought the small Labyrinthodonts of Linton, Nýřany, and elsewhere into his account in an admirable and illuminating manner.

The present paper is an attempt to isolate a single evolutionary group, long lived, elaborate and world wide, but always recognizable by special structural details found nowhere else. I have work in progress, in a relatively advanced stage, on the immense material of the Capitosaur series.

In 1915 Robert Broom examined the British Museum type skulls of Owen's *Brachyops laticeps* (1854) and Huxley's *Bothriceps australis* (1859). He had himself described *Batrachosuchus browni* (1903), and now pointed out the resemblance between these three animals, founding for them a new family—Brachyopidae—without giving any distinctive characters of the group.

In 1919 I described the structure of the posterior part of the palate of *Bothriceps*, and gave a more complete account of the skull of *Batrachosuchus*. With these forms I brigaded Jaekel's genus *Plagiosaurus* (1914), founded for *P. depressus* from Halberstadt, to which he had added Fraas's *Plagiosternum pulcherrimum* (1913) and Fraas's *Plagiosternum granulosum* (1889), Jaekel having made for these three forms an " order " Plagiosauri, without giving any definition of the group.

I defined the group by saying that its members resemble one another, and differ from all known Stereospondyl types, in the following ways :

(1) The broad parabolic skulls with large anteriorly situated orbits.

(2) The unusual way in which the proötic flange of the squamosal wraps round the outer side of the quadrate, and having formed a laterally concave face on the occipital surface, ends in a ridge, separated from an exactly similar ridge of the pterygoid by the quadrate.

(3) The upturning of the lateral wings of the pterygoids from the subtemporal fossae, so that the palate forms a broad ∩-shaped arch.

(4) The unusual way in which the posterior edge of the pterygoid is applied to the inner face of the quadrate.

(5) The occipital condyles lie far behind the dermosupraoccipitals so that the occipital surface slopes forward.

I pointed out that the then undescribed *Dvinosaurus* possessed all these five qualities, but was a primitive rhachitomous form. No subsequent author (except Sushkin, 1936) appears to have paid any attention to the list of diagnostic characters of the Brachyopids set out above, perhaps because I did not publish a series of drawings illustrating the matter.

Subsequently *Dvinosaurus* was described and figured by Amalitzky (1924), by Sushkin (1923, 1936), and by Bystrow (1935, 1938), the last two bringing out the neoteny which it shows, and the last producing an admirable account of the whole skeleton.

The later Brachyopids have been described and discussed by von Huene (1922) and Tage Nilsson (1934, '37, '39, '45), and A. S. Romer has treated them in his *Review of the Labyrinthodontia* (1947). He accepts the Brachyopidae and the group Plagiosauridae for the extreme forms, but adds the Metoposaurs to the assemblage, whilst removing *Dvinosaurus* to the neighbourhood of *Trimerorhachis* and " *Saurerpeton* ". There is thus some variety of opinion about the whole matter and further treatment of it is necessary.

The Brachyopids proper are rare animals known usually from the occurrence of single individuals of each species from rocks of Upper Permian and Lower Triassic age in Australia, India, South Africa and Argentina, and the published accounts of their structure are inadequate.

BRACHYOPIDS PROPER

Survey of Group

The Brachyopids include a terminal group of Middle and Upper Triassic forms, the Plagiosauridae, but its typical members are from earlier beds whose age relations are unfortunately not very accurately known. The complete list of these is as follows :

(i) *Brachyops laticeps* Owen. The type—and only known specimen—was found in the " Mángali beds " at Mángali, in Nagpur, Central India. This horizon is assumed on poor evidence to be equivalent to the Panchets (C. S. Fox, 1931 : 159). The age of the Panchets is to be determined from their fauna of vertebrates, and from a considerable flora. The fauna has recently been described by von Huene (1942) who recognizes in it a genuine *Lystrosaurus* and remains of *Chasmatosaurus*, genera otherwise known only in the Lystrosaurus zone of South Africa and of Sinkiang. Furthermore he has described a skull of the Labyrinthodont *Gonioglyptus*, which genus occurs in the Panchets, from the Prionolobus beds of Chideru in the Salt Range. I am not, however, convinced that the generic identity of the two animals is established. The important member of the flora is *Glossopteris*, which seems to be the commonest form, and is accompanied by its stem " Vertebraria ", so that the generic determination may be regarded as certain. It is primarily a Permian form, found in South Africa from the Ecca upward, though it probably does not occur in the Cynognathus zone flora of Aliwal North. In Australia it is abundant from the Lower Marine series up through the Coal Measures of Newcastle, but it probably does not occur in the Narrabeen shales—or higher. Thus it can probably be assumed that *Brachyops* is of Lystrosaurus zone age.

(ii) *Bothriceps australis* Huxley. The type—and only known specimen—was bought by the British Museum in 1848 from a person of whom nothing is known, and was then said to have been found in " Australia ".

(iii) " *Platyceps* " *wilkinsoni* Stephens. There were several described specimens from the well known fish bed of Gosford, New South Wales, which lies in a sandstone member of the Narrabeen shales. One specimen was on loan to the British Museum (Natural History) about 1920–24, when I had a photograph made from it. Its age is relatively well determined ; it is in a formation immediately followed conformably by the Hawkesbury sandstone, from which came the well-preserved fish fauna of Brookvale, described by R. T. Wade in 1935. This fauna is directly comparable with that from Bekker's Kraal in the Cynognathus zone of South Africa, and thus appears to be Lower Triassic.

(iv) "*Bothriceps* " *major* A. S. W. (*non* Owen) comes from a " coal "—actually a torbanite—at Airly, Central Coalfield, New South Wales. This lies in the " Upper Coal Measures ", a formation succeeded by the Narrabeen shales. It is therefore of pre-Triassic age, and may be nearly contemporary with *Brachyops*, or perhaps a little older, in the definitely Permian Cistecephalus zone.

(v) *Batrachosuchus browni* Broom comes from Aliwal North, Cape Province, South Africa, presumably from the Cynognathus zone, Lower Trias.

(vi) *Batrachosuchus watsoni* Haughton comes from an unknown locality certainly in the Cynognathus zone of the Burghersdorp district.

(vii) *Pelorocephalus mendozensis* Cabrera comes from rocks at Potrerillos, Mendoza, Argentina, which on inadequate evidence are regarded as of Upper Middle Triassic age.

Thus in order of age the Brachyopids are :

Rhaetic—*Gerrothorax, Plagiosaurus.*
Upper Trias—*Gerrothorax, Plagiosternum, Plagiosuchus.*
Middle Trias—*Plagiosuchus,* ? *Pelorocephalus.*
Lower Trias—*Batrachosuchus, Platyceps.*
Basal Trias, or Uppermost Permian—*Brachyops.*
Upper Permian (Cistecephalus zone)—"*Bothriceps*" *major.*

Its own structure suggests that *Bothriceps australis* is as early as, or earlier than "*Bothriceps*" *major*. *Dvinosaurus* from the Cistecephalus zone of Russia is presumably of much the same age as "*Bothriceps*" *major*, and may well have been contemporary with *Bothriceps australis*, or indeed younger.

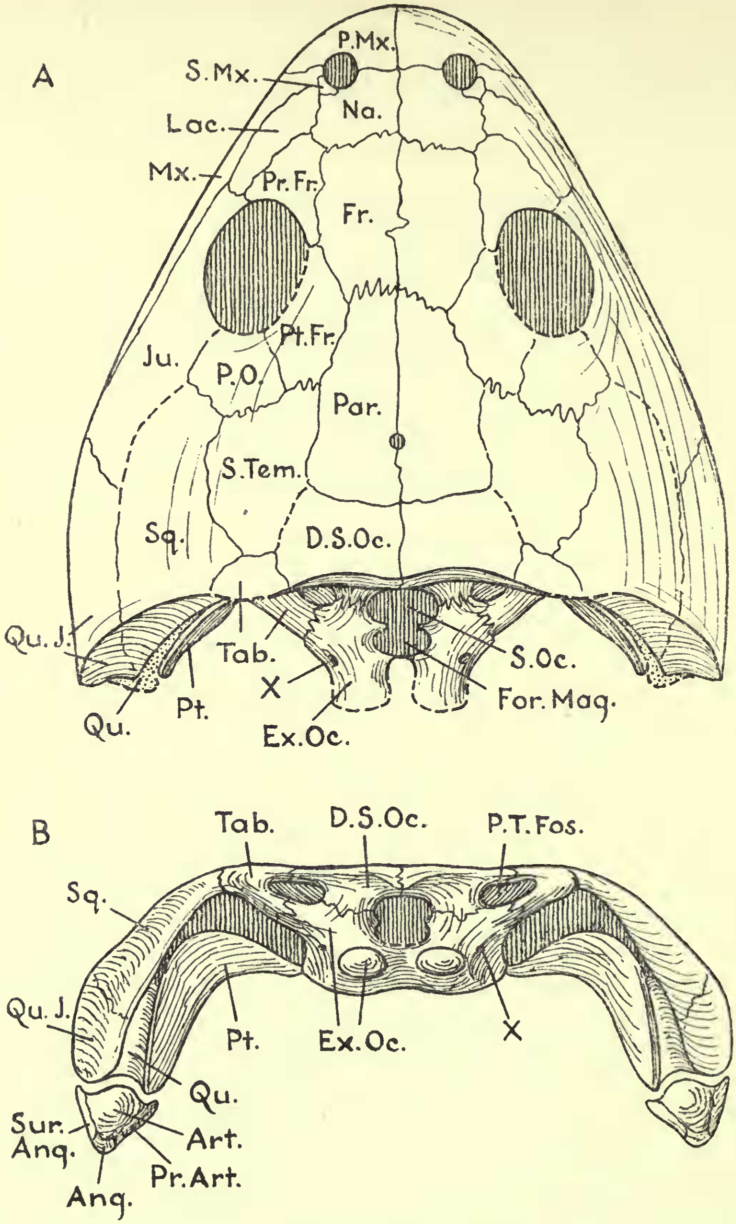
Bothriceps australis Huxley

The unique type specimen (B.M.N.H., 23110) consists of a skull with the lower jaw tightly closed on it. The whole upper and lateral surface is preserved as a beautiful internal cast, showing the details perfectly, except for some lost regions. To this cast a little actual bone adheres in places and shows, perfectly preserved, the outer surface over small areas, including a lachrymal. The occiput, though damaged, remains as well-preserved bone, and the palate (further developed since 1919) is excellently preserved. Both lower jaws are complete and well shown.

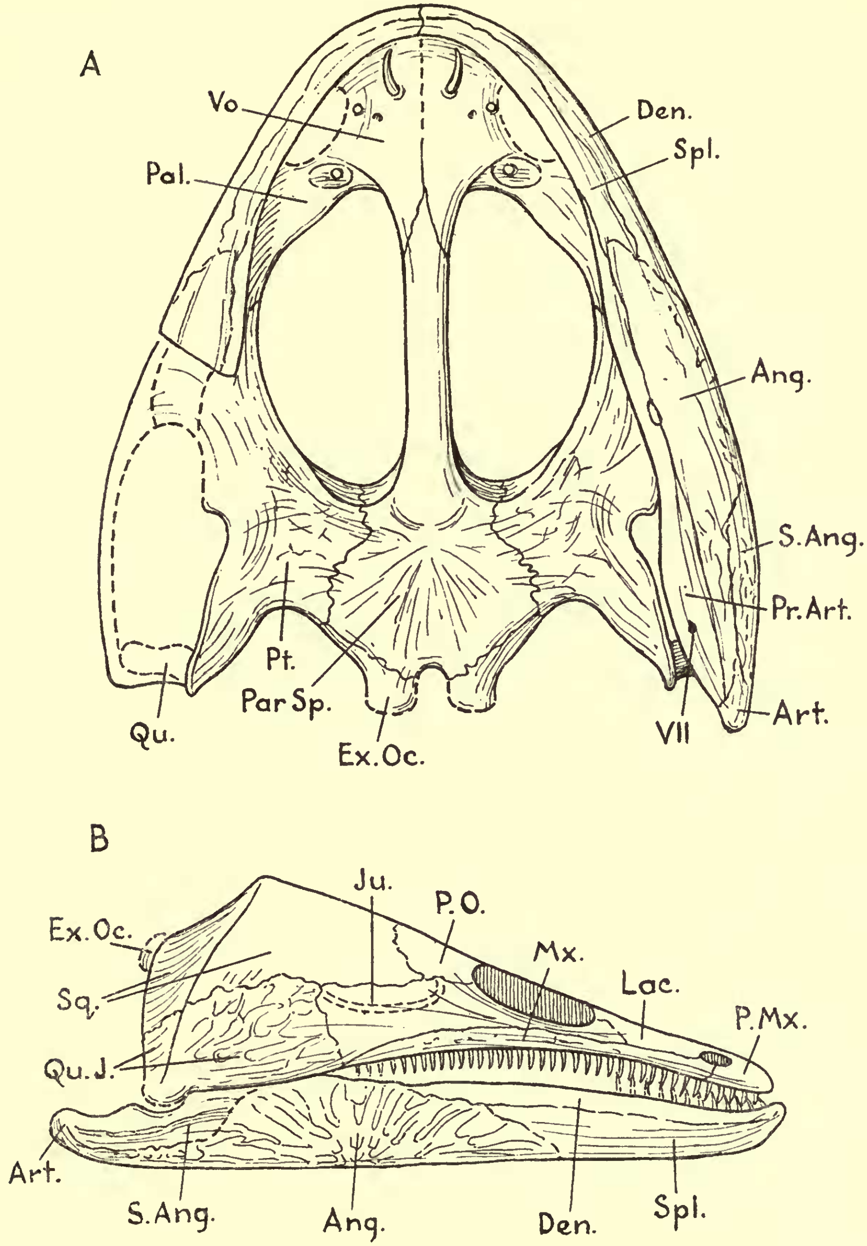
The skull is parabolic in plan and about 15% wider than its length, measured on the skull table. On the left side of the specimen it can very clearly be seen that as far back as the orbit the anterior part of the skull is very much depressed, its ventral border then turning downward so that the skull becomes very deep at the occipital border. The orbits lie almost entirely in front of the mid length, and are comparatively small, so that the face is long for a Brachyopid. The hinder border of the dermal roof is damaged at the lateral end of the tabular, but it seems obvious that there can have been no real otic notch ; indeed there may not have been any embayment at all. The dermosupraoccipitals have a well-marked posterior border on the upper surface, behind which they are produced downward on to the sloping occipital surface by lappets which rest on and end in a suture with the exoccipitals.

The tabulars are short but wide, having a long suture with the supratemporal and the squamosal. They have long occipital flanges passing downward and inward below the large post-temporal fossae to meet the exoccipitals in suture.

The shapes and relations of the main bones of the skull roof can best be understood from Text-figs. 1 and 2. The more important features to which attention should be drawn are : there is a septomaxilla, clearly shown as a small triangular area of bone surrounded by sutures, which is attached to the nasal and lachrymal behind the nostril. The lachrymal is shown on both sides of the skull ; in part the sutures



TEXT-FIG. 1.—*Bothriceps australis* Huxley. Type specimen (B.M.N.H., 23110) slightly restored. Natural size. A, Dorsal surface; B, occipital view, with lower jaw in place. The detailed shape of the bones on the skull roof comes nearly entirely from the impression of their under surface, thus the fragments of lateral line grooves shown on the outer surface of the right premaxilla, left lachrymal, and right jugal and squamosal are not represented. *Ang.*, angular; *Art.*, articular; *D.S.Oc.*, dermosupraoccipital; *Ex.Oc.*, exoccipital; *For. Mag.*, foramen magnum; *Fr.*, frontal; *Ju.*, jugal; *Lac.*, lachrymal; *Mx.*, maxilla; *Na.*, nasal; *P.Mx.*, premaxilla; *P.O.*, postorbital; *P.T.Fos.*, post-temporal fossa; *Par.*, parietal; *Pr.Art.*, prearticular; *Pr.Fr.*, prefrontal; *Pt.*, pterygoid; *Pt.Fr.*, postfrontal; *Qu.*, quadrate; *Qu.J.*, quadratojugal; *S.Mx.*, septo-maxilla; *S.Oc.*, supraoccipital; *S.Tem.*, supratemporal; *Sq.*, squamosal; *Sur.Ang.*, surangular; *Tab.*, tabular; *X*, tenth cranial nerve foramen.



TEXT-FIG. 2.—*Bothriceps australis* Huxley. Natural size. A, Ventral surface, showing imaginary removal of the hinder part of the right mandible ; B, right lateral aspect, showing ornament and lateral line groove where preserved. The lower jaw is restored to its natural position by being lowered so that the quadrate articulated with it regains its original place, and the ornamented outer surface of the angular does not underlie the quadratojugal. The projection of the dentary in front of the premaxilla and the backward direction of its anterior teeth are as in the specimen. Reference letters as before with : *Den.*, dentary ; *Pal.*, palatine ; *Par.Sp.*, parasphenoid ; *Vo.*, vomer ; *VII*, foramen for seventh cranial nerve (chorda tympani).

surrounding it are shown on the outer surface of the bone, elsewhere on the mould of the inner surface. The bone does not enter the margin of the nostril, but it is possible that it does form a very small part of the orbital margin. It is entirely surrounded by the maxilla, septomaxilla, nasal, prefrontal and jugal. The pre- and postfrontals meet in suture above the orbit. The jugal forms the whole lateral margin of the orbit, articulating in front with the pre-frontal ? and lachrymal. The large supratemporal meets the postfrontal and postorbital anteriorly, and the dermosupraoccipital and tabular behind. The squamosal is represented mainly by an internal impression, but some bone is preserved. It has a large superficial exposure of ornamented bone ending behind at a definite margin round which the bone turns on to the occipital surface. Here it forms a smooth face standing nearly vertically, and concave on a vertical axis, so that its admesial border is turned backward ending parallel with, but separated by a narrow space from, the hinder border of the quadrate ramus of the pterygoid. This space was obviously occupied by a cartilaginous ridge arising from the visible occipital surface of the quadrate. The quadratojugal is a relatively large bone, lying below and continuing the surface of the squamosal, and extending forward to meet the jugal. That part of it which lies on the outer surface has a normal labyrinthodont ornament, the occipital area being smooth.

The occipital surface is preserved in bone, but is much damaged by weathering and fracture. None the less its structure can easily be made out, and it is represented in Text-fig. 1. The occipital surface slopes backward for a long distance (its own height) behind the ridge on the dermosupraoccipital which marks the hinder border of the skull table. There is no bony basioccipital, but a space which must have been occupied by it exists dorsal to the hinder end of the parasphenoid and between the roots of the exoccipital condyles. The existence of a cartilaginous supraoccipital is shown by the usual shelves on the exoccipitals. The exoccipital condyles are broken off, and the broken surface polished, but they were evidently transversely widened and had a considerable projection backward. The main body of the bone extends upward to meet the occipital lappet of the dermosupraoccipital in a suture, then outward to a suture with the occipital flange of the tabular, forming the lower border of a post-temporal fossa, and evidently sheathing the posterior surface of a cartilaginous paroccipital. The lower part of the bone there passes forward in contact with the upper surface of the lateral border of the parasphenoid to end in a contact with the pterygoid. The exoccipital is perforated by a foramen for the vagus, but it is impossible to be sure whether or not a hypoglossal foramen existed.

The palate, after further preparation by Mr. L. E. Parsons, is well exposed on the left side of the skull, although the adherent lower jaw hides its lateral portions. The parasphenoid has a processus cultriformis with a flat ventral surface which expands into a widened body whose lower surface is also flat, though it is crossed by two shallow grooves which meet in the middle line. It ends in a shallow notch between the pedicels of the exoccipital condyles, the bone is then in contact with the exoccipital by a nearly straight suture extending outward and forward to meet the long one between the parasphenoid and pterygoid. This suture has a rather characteristic sinuous course which can be seen in Text-fig. 2, A. There is no transverse ridge corresponding to that which in *Capitosaurus* represents the pockets for the recti capitis muscles. The pterygoid at its attachment to the parasphenoid is flat, and this horizontal surface extends outward until it rather suddenly turns downward to end at the margin of the subtemporal fossa. The vertical wall so formed extends backward to lie in contact with the admesial surface of the quadrate, so that a thin strip of that bone, and its cartilaginous dorsal continuation, separate it from the corresponding inner flange of the squamosal. It is evident that the lower part of the wall was a sheath covering the inner side of the masticatory muscles. The inter-pterygoid vacuities are large, their anterior margins lying in the palatines and vomers. There is an alternative pair of large teeth on the palatine, and one very laterally placed on the vomer. The border of the internal nostril is not shown.

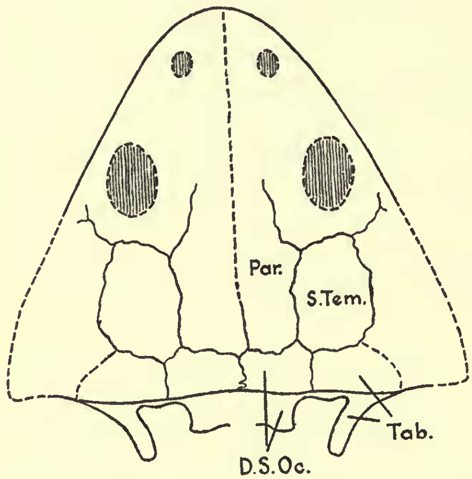
The lower jaw is in postion with the mouth shut. In the specimen the teeth at the front end of the lower jaw lie in front of those in the premaxillae, and much of the maxilla lies mesial of the dentary tooth row. How far this condition is natural I do not know. The lower jaw is shallow and wide. Its ventral surface is straight and there is a large retro-articular process made from the articular, covered laterally by the surangular and angular, and mesially by a prearticular which, just anterior to the articulation with the quadrate, is perforated by a foramen for the chorda tympani. A small Meckelian foramen between the prearticular and angular lies on the inner surface just above the ventral border of the jaw.

"Bothriceps major" A. S. W. = Trucheosaurus gen. nov.

The type specimen of *Bothriceps major*, found at Airly in an "oil shale" in the Newcastle Coal Measures of the Central Coalfield of New South Wales, is a large part of a skeleton, one surface being on B.M.N.H., R.3728, whilst the counterpart is in Sydney, New South Wales. The slab in which it is preserved is a bog-head or torbanite, no doubt made largely of the alga *Reinschia*. This material was certainly deposited on the floor of a lake or pool, and the animal must have sunk on to it whilst still nearly (or quite) complete. It has preserved the bones extremely badly, little of them remaining except as a buff coloured film of very small thickness. Thus no preparation is possible.

The specimen in London now consists of two blocks. One contains the head, broken so that the left hinder corner is lost and the occiput is incomplete. The other shows a series of 28 vertebrae and their ribs, no trace of the shoulder girdle remaining. This block extends beyond the preserved part of the vertebral column.

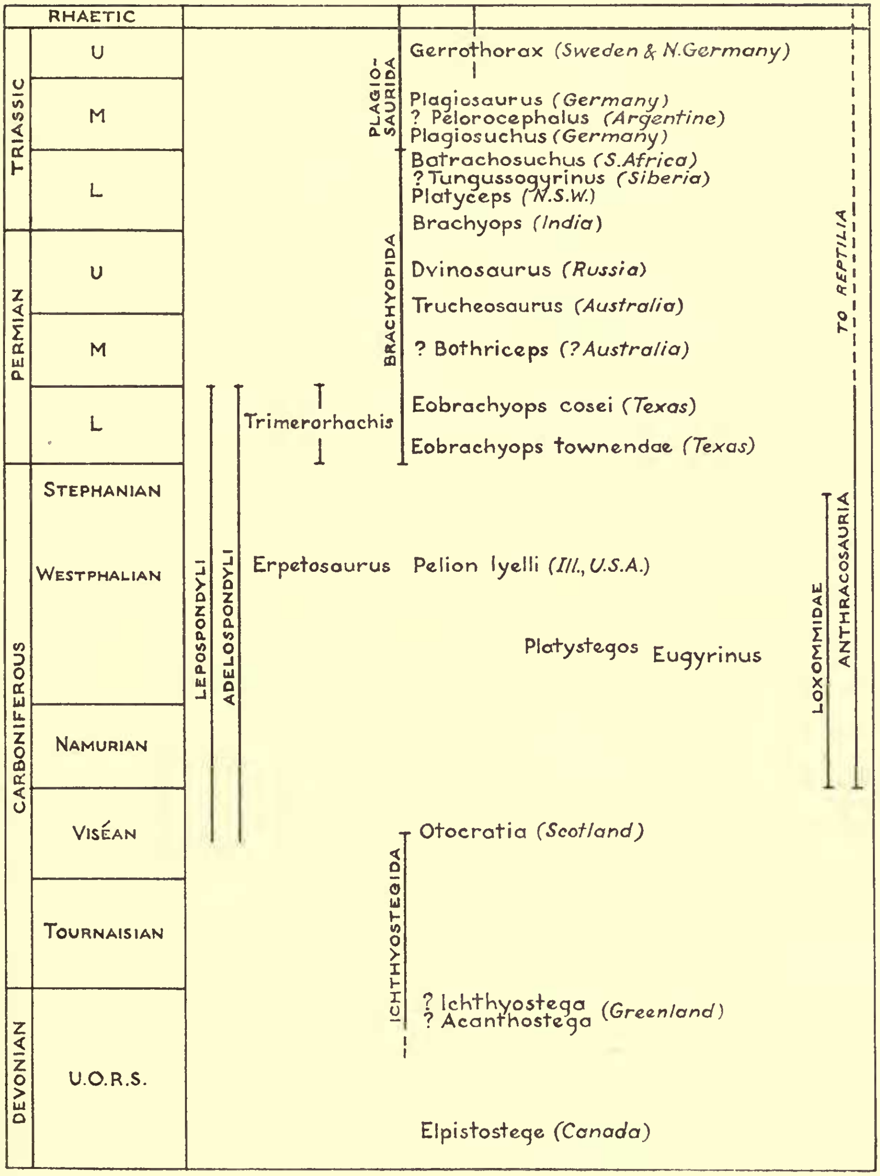
The head and lower jaw are dorsoventrally compressed, and only a faint impression of the upper surface remaining on the slab can be interpreted. The general shape is evident, but it is impossible to be sure of the position of the orbits. The almost straight hinder edge of the dermal roof of the skull is certain, and the lappets of the tabular and dermosupraoccipital which extend backward on to the sloping occiput are well shown. The sutures shown in Text-fig. 3 are derived mainly from the abrupt changes of direction of the ridges which form the ornament of the bones of the skull roof, and these are in all probability a close approximation to the facts. There are no visible traces of lateral line grooves. This skull is evidently that of a Brachyopid : the shortness, great width, presumed anterior position of the orbits, and especially the absence of any otic notch, and straight occipital margin of the skull roof, with the long projection of the occipital surface behind the roof—all facts which are clearly shown and certain—are to be found only in this group of Labyrinthodonts. A small piece of matrix surrounding the occipital process of the tabular and the hinder border of the squamosal on the right side remains. Had the specimen possessed ossified branchial arches some parts of them would have been expected to be preserved in this area, but as there are no such traces visible it is probable that the species was not neotenous. Thus the Brachyopids existed in a typical form in the Upper Permian, presumably in the Cistecephalus zone.



TEXT-FIG. 3.—*Trucheosaurus* ("*Bothriceps*") *major* (A. S. W.) (B.M.N.H., R.3728). Diagram of skull roof. × ⅓. Reference letters as before.

The remainder of the skeleton shows little. The vertebrae are so crushed dorso-ventrally that nothing can be said about them, except that they do not seem to have had the solidity and close approximation of those of the latter Plagiosuchids. The ribs are parallel-sided, little curved, and short—consistent with a broad, dorso-ventrally flattened body. There is evidence of some 28 vertebrae, and their pairs of ribs, preserved; the slab containing the shoulder region is likely to have held 5 more; the series ends before there is any sign of a pelvis and hind legs, which must have lain even further back, although the preserved and inferred part of the backbone is three and a half times as long as the skull. A misplaced fore leg shows a humerus less than a quarter of the skull length in its bony extent, and shorter radius and ulna.

That *Bothriceps major* A. S. W. is a Brachyopid is thus certain, but in the few structures clearly shown in the only known specimen it differs from the type of the genus *Bothriceps*, and indeed from all other known genera of the family. It is thus desirable to place it in a new genus, but the specimen is so poorly preserved that it is quite probable that a well preserved skull of the same species might not be recognizable as such, so that any new genus founded for the specimen would naturally remain without adequate definition. But the specimen is important as showing the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? Pelorocephalus (Argentine)
Plagiosuchus (Germany)
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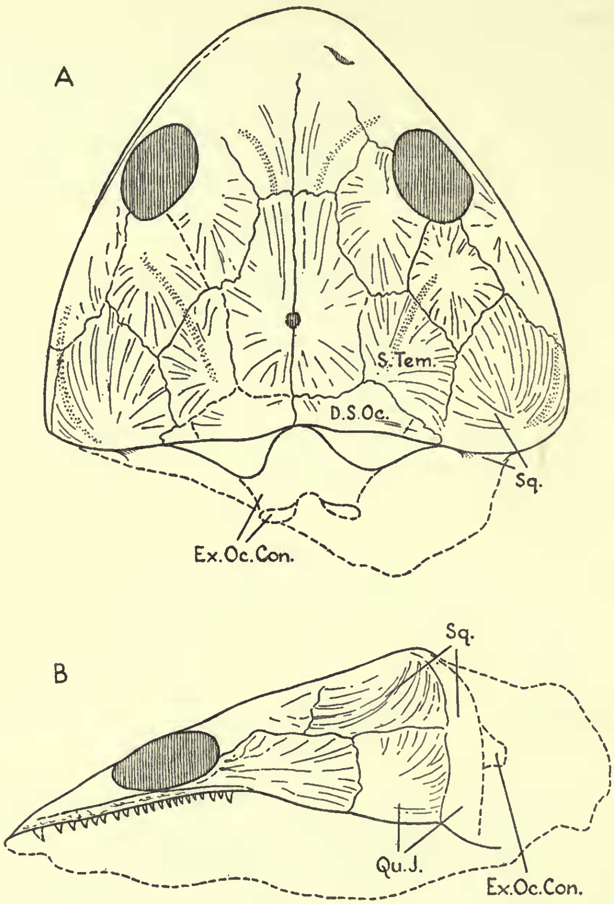
Platyceps (N.S.W.)
Brachyops (India)
Dvinosaurus (Russia)
Trucheosaurus (Australia)
? Bothriceps (?Australia)
Eobrachyops cosei (Texas)
Eobrachyops townendae (Texas)
Trimerorhachis
LEPOSPONDYLI
ADELOSPONDYLI
Erpetosaurus
Pelion lyelli (Ill., U.S.A.)
Platystegos
Eugyrinus
TO REPTILIA
LOXOMMIDAE
ANTHRACOSAURIA
Otocratia (Scotland)
ICHTHYOSTEGIDA
? Ichthyostega
? Acanthostega
(Greenland)
Elpistostege (Canada)

occurrence of a typical Brachyopid at an early horizon, and it must have a generic name for reference, for which I propose *Trucheosaurus* (Gr. *τρυχεα*, rags and tatters).



TEXT-FIG. 4.—*Brachyops laticeps* Owen. Type specimen (B.M.N.H., R.4414). × ½. A, Direct dorsal view; B, lateral view, without reconstruction, dotted outline is that of the matrix. Reference letters as before, with: *Ex.Oc.Con.*, exoccipital condyle.

BRACHYOPS LATICEPS Owen

The unique type specimen of *Brachyops laticeps* Owen (B.M.N.H., R.4414) was found at Mángali, Nagpur, Central India, in beds of uncertain correlation but of probable basal Triassic age.

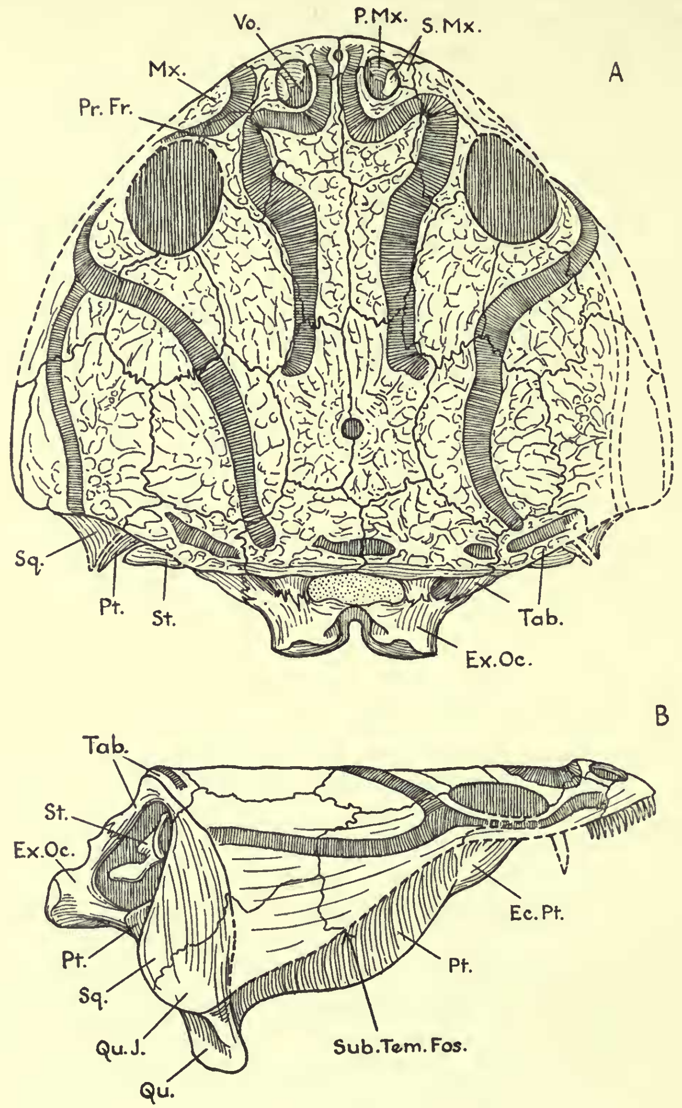
This skull, which lacks a lower jaw, is contained in a curious pink-coloured fine-grained rock, and has very nearly retained its original shape, though the right side is slightly crushed downward and outward. The preservation is unusual and bad. The actual bone seems to have lost its structure; even when seen in transverse section the hinder ramus of the pterygoid is thin and not recognizable under a lens as bone. The superficial ornament of the upper surface is recognizable, though preserved in unnaturally low relief, and imperfectly. The right orbit is well defined, but the position of the pineal foramen is uncertain. The preorbital part of the skull shows its outline, and a possible stretch of the border of the nostril, but is otherwise unintelligible. Sutures are occasionally visible, but must often be inferred from the radiate ornament of the individual bones. Lateral line grooves are sometimes evident. The occiput is present, badly preserved The structure of the dermal skull roof is obvious from Text-fig. 4, A and B, in which the projection of the occiput is certainly fixed, as is the width across the occipital condyles. The characteristic straight occipital border and absence of otic notches are certain, and the specimen shows clearly on both sides the swinging round of the squamosal on to the hinder surface and its termination at a backwardly turned ridge, clearly seen on the left side to be separated by a narrow space of nearly constant width from the hinder edge of the pterygoid seen in section. This space obviously received a cartilaginous ridge on the posterior surface of the quadrate. The lateral line grooves, whose distribution is shown, are relatively narrow, unlike those of *Batrachosuchus*.

In side view (Text-fig. 4, B) it is evident that the hinder part of the maxilla lower (tooth bearing) border is turned a little downward, the lower border of the jugal and quadratojugal continuing its trend. (Dinkel's admirable drawings (Owen, 1855) do not bring this point out clearly, presumably because of some foreshortening by use of a camera lucida.)

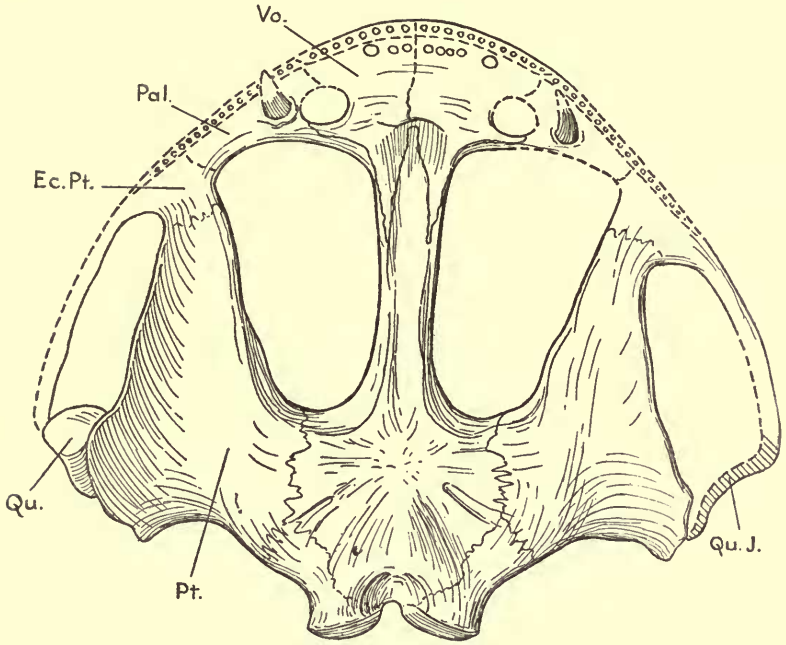
BATRACHOSUCHUS WATSONI Haughton

The genus *Batrachosuchus* was founded by Broom for *B. browni*, an excellent skull found by Alfred Brown in the Cynognathus beds of the Aliwal North district, Cape Province, South Africa. The only other material is a skull, B.M.N.H., R.3589, from the Seeley collection, which is without any record of origin, but almost certainly came from the Cynognathus zone of the Burghersdorp district. I gave a description of this skull in 1919, and S. H. Haughton subsequently (1925) made it the type of *B. watsoni*. This skull is nearly complete and most perfectly preserved. It is quite undistorted and shows all details of the bones in perfection, but unfortunately the lateral borders of the orbits have been broken away and lost, and the lower parts of the jugals and quadratojugals have been removed, leaving however an impression of the inner surfaces which shows the lower border of the skull with certainty. In my original description I illustrated the skull roof only by a photograph, which was taken at the British Museum in my absence. This was evidently made with a vertical camera, the skull resting on the tip of the quadrate, and on a piece of matrix which supports the premaxillary teeth, when the skull roof lies at an angle of more than 30 degrees with the horizontal. Thus my published photograph is foreshortened, and exaggerates the projection of the occiput and shortness of the skull in relation to its width.

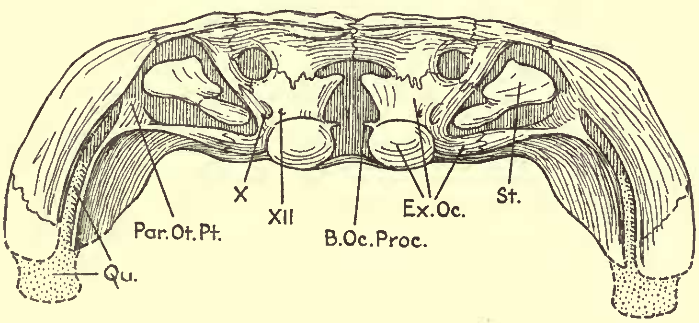
The pattern of the dermal bones of the skull roof is shown in Text-fig. 5 in which it is seen at right angles to its plane, and to the sagittal plane of the skull from a distance



TEXT-FIG. 5.—*Batrachosuchus watsoni* Haughton. Type specimen (B.M.N.H., R.3589). $\times \frac{4}{9}$. A, Direct view at right angles to dorsal surface, essentially unrestored; B, direct lateral view. The broken line lower border of the temporal region from the hinder end of the maxilla backward follows an impression of the visceral surface of the bones, and is certain. (The quadrate, though shown in solid line, is considerably eroded). Reference letters as before with: *Ec.Pt.*, ectopterygoid; *St.*, stapes; *Sub.Tem.Fos.*, subtemporal fossa.



TEXT-FIG. 6.—*Batrachosuchus watsoni* Haughton. Type specimen (B.M.N.H., R.3589). × ½. The palate, viewed at right angles to the parasphenoid. Reference letters as before. *Qu.J.* is a transverse section of the quadratojugal where it turns inward behind the quadrate to form the characteristic concave surface found only in Brachyopids. It is drawn as it exists in the specimen.



TEXT-FIG. 7.—*Batrachosuchus watsoni* Haughton. Type specimen (B.M.N.H., R.3589). × 4/9. The occiput seen directly from behind with the upper surface horizontal. Reference letters as before with : *B.Oc.Proc.*, process of exoccipital over the basioccipital cartilage and below the brain cavity ; *Par.Ot.Pt.*, the parotic part of the pterygoid as now exposed, it may reach the skull roof, and extend far in.

of about 100 cm. The only region where the skull roof pattern presents any difficulty is that between the nostril and the orbit. The structure of the premaxillae is obvious; they meet in the middle line, a small opening—perhaps for an interpremaxillary gland—interrupting the suture. They are attached to the anterior ends of the nasals, the two bones together forming the anterior, mesial and hinder borders of the somewhat asymmetrical nostrils. On each side the margin of the nostril is completed by a small bone attached by obvious sutures to the lateral part of the premaxilla in front, and to the lateral part of the nasal behind. These bones are ornamented, each bearing a small knob on its upper surface anteriorly, that on the left having further ornament posteriorly. On the left side I excavated the nostril to its floor, exposing the smooth upper surface of the vomer (separated by a distinct suture from the premaxilla) and found that the bone now under discussion descends from the outer border of the nostril to expand into a small flat sheet resting on the upper surface of the vomer. The posterior end of the vertical part of the bone is notched, and it is clearly a septomaxilla, a simple modification of the ordinary labyrinthodont type.

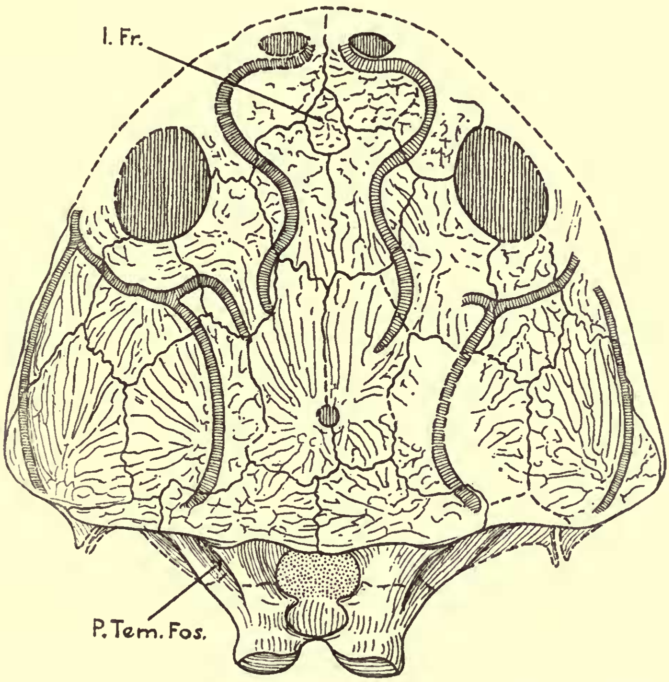
The anterior part of the maxilla is perfectly preserved on each side, its lower border, and the teeth which it bears, being visible on the left side. From here its very highly sculptured surface can be traced upward to an obvious suture with the premaxilla, septomaxilla, nasal and prefrontal. There is thus no sign of a lachrymal; either the bone has fused early in life with the maxilla—which is improbable—or it has vanished, squeezed as it were out of existence by the approximation of the nostril and orbit.

Nothing further in the structure of the skull roof calls for notice here; the whole pattern is determined with certainty. The noticeably anterior position of the quadrates, obscured in my early photograph, is important.

The lateral aspect of the skull (Text-fig. 5, B) brings out its extraordinary shape. The preorbital region is low, there being in fact only a space of some five millimetres in height separating the upper surface of the vomer from the lower surface of the nasal at the hinder margin of the nostril. The depth of the skull at the orbit is much less than the length of that opening, and unless the eye were very small it must have projected far above the skull roof, like that of a frog, and, like the frog's, have been capable of retraction through a special lateral bay in the interpterygoid vacuity. It is remarkable that the orbital margin is not at all everted as is that of *Capitosaurus*. Behind the orbit the skull rapidly deepens until at the quadrate it is remarkably high. The dorsal surface is flat, but it seems evident that there was a break in the direction of the ventral border of the skull roof about at the back of the orbit, the lower margin of the maxilla lying nearly parallel to the skull roof, whilst that of the jugal and quadratojugal lies at an angle of some 40 degrees to it. Thus, as shown in my original figure of the occiput, the quadrate condyle is placed very ventrally, lying far below the ventral surface of the basis cranii.

The posterior border of the skull roof is clearly marked by a ridge which, crossing the flat table, passes outward and downward at the hinder end of the ornamented surface of the squamosal and quadratojugal The smooth hinder surfaces of these bones pass inward and backward round a concave cylindrical surface to end in a free margin, attached to a ridge on the hinder surface of the quadrate bone and its cartilaginous dorsal extension. This ridge is supported on its admesial side by the hinder edge of the pterygoid.

The ornament of the skull roof is of normal labyrinthodont pattern consisting of pits—usually round and separated by low ridges with rounded upper surfaces—but in some regions elongated into short grooves. It is an interesting confirmation of Bystrow's view that the areas with grooved ornament represent regions of relatively large growth in the direction of the grooves, that the grooves on the skull of *B. watsoni* seldom run antero-posteriorly, but often transversely. They are best marked where



TEXT-FIG. 8.—*Batrachosuchus browni* Broom. Drawn (with some of the bones put back into place) from a cast of the type skull in Cape Town. × ½. *I.Fr.*, interfrontal; *P.Tem.Fos.*, post-temporal fossa.

they run into the suture between the supratemporals and the squamosals—implying a widening of the skull here—and on the postorbital at its suture with the squamosal, which in continuation of them has very small round pits, suggesting that in youth the postorbital was wedged in between the squamosal and supratemporal. Through this normal ornament the lateral line grooves make their way as wide but shallow troughs, usually very broadly V-shaped in section. Their flanks often bear close set, low, transverse ridges. They are very extensively developed, with a normal distribution, though there is a possible transverse groove on the left tabular to which it is difficult to find a parallel.

The occiput was correctly shown in my figure 28 (1919), but further preparation has been made of the left stapes. This is now shown to rise more nearly to the under-surface of the tabular at the admesial end of its upper border, so that the depth of the bone is increased above the notch for a blood vessel, and the ventral surface of the inner end is widened and its anterior part produced downward as a flange which presumably had a sutural attachment to the outer border of the parasphenoid. The pterygoid is shown to have a parotic plate reaching upward toward the cranial roof, on the inner surface of the quadrate from the upper side of the horizontal shelf which projects into the exoccipital and parasphenoid.

Batrachosuchus browni Broom

This species is still represented only by the type specimen, which, when Broom described it, was a split slab (? nodule), one side of which showed the visceral aspect of the roof of the skull, the other had been prepared by him to show the palate. Subsequently the South African Museum replaced the skull roof and prepared the ornamented outer surface, which, though a little broken and misplaced, is beautifully preserved; only the quadratojugals and anterior part of the face are missing. Its structure is shown in Text-fig. 8.

It differs from *B. watsoni* in being proportionately longer and narrower, with the eyes further back, and in the greater projection of the occipital condyles behind the occipital border of the skull roof.

The lateral line grooves have the same general distribution as in *B. watsoni*, but are actually and relatively much narrower and of more U-shaped section. There is a peculiar inwardly and backwardly directed branch of the supratemporal line on the hinder part of the postorbital, absent in *B. watsoni*.

The shapes of the individual bones of the skull roof are essentially the same, though *B. browni* has an interfrontal bone between the frontal and nasals.

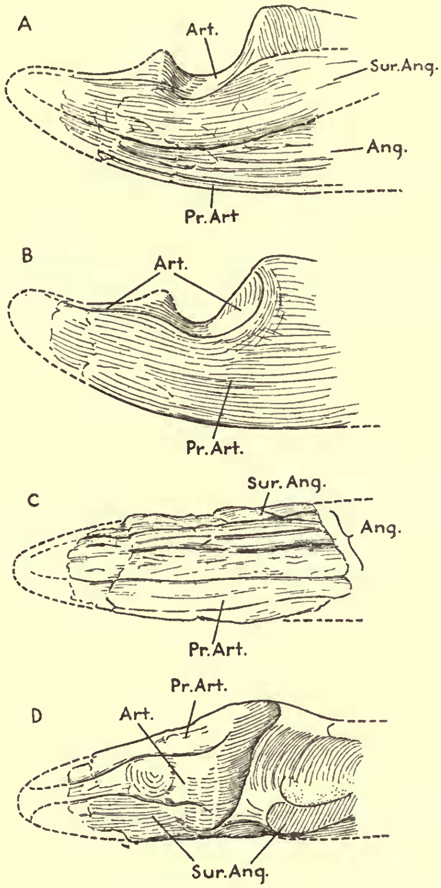
? Batrachosuchus sp.

In 1911 I collected three fragments of labyrinthodont jaw (D.M.S.W., B.126) and an atlas (D.M.S.W., B.140) from a small weathered slope of shale of the Cynognathus zone by the roadside on the farm Luiper Kop between Burghersdorp and Knapdaar Two of the jaw fragments fit together to make the very weathered posterior end of a right mandible, the other is part of the left ramus (including the front half of the articulation) evidently of the same individual; right and left sides supplement one another and show the structure well.

The essential features (Text-fig. 9) are that the jaw is low, nearly as wide as high at the articulation, with a well formed articular face behind which a long process stretches backward. This has a core of articular, forming a median strip of its upper surface, which is bordered by surangular and prearticular, the angular sheathing a strip of its lower and outer surface. The details of structure differ greatly from those of Capitosaurs, *Benthosuchus*, and the Spitsbergen Trematosaurs described by Tage Nilsson, and there can be no real doubt that the jaw (which much resembles those of

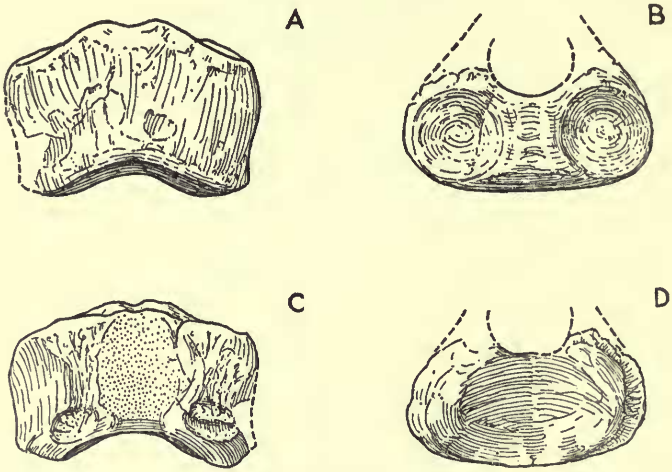
Bothriceps, *Pelorocephalus* and *Dvinosaurus*, and is comparable with that of *Eobrachyops*) is that of a Brachyopid. If it be then presumably it belongs to *Batrachosuchus*, which it fits quite well.

Remains of amphibia are so rare in the Cynognathus zone that " association " of labyrinthodont fragments found close together is usually justified, and I therefore



TEXT-FIG. 9.—? *Batrachosuchus*. (D.M.S.W., B.126). × ½. Posterior part of a lower jaw, a little restored from fragments of each side. A, Right ramus, outer surface ; B, left ramus, inner surface ; C, right ramus, ventral surface ; D, right ramus, dorsal surface. *Ang.*, angular ; *Art.*, articular ; *Pr.Art.*, prearticular ; *Sur.Ang.*, surangular.

describe the atlas found with these jaw fragments as that of *Batrachosuchus*? The atlas (Text-fig. 10), partly covered with a thin haematite film, is much weathered, not completely prepared, and has lost its neural arch. But it is a single bone, only about half as high as it is wide with a laterally concave posterior surface, widening a little anteriorly. The anterior face bears two shallowly spheroidal hollows for articulation with exoccipital condyles which are separated by a rather wide, slightly hollowed and pitted surface. The floor of the cavity for the spinal cord is wide and somewhat depressed over its length ; the roots of the neural arch are, so far as can be judged, extremely slender. The lower surface of the bone is pitted by irregular, often longitudinal depressions. The specimen measures 4·8 cm. across the condylar depressions. The condyles in *B. browni* are 6·0 cm. across. In *B. watsoni* the corresponding width is 5·0 cm., only a few millimetres greater than that of the atlas, and the same depth. The only important recognizable feature is the absence of any indication that the atlas was ever more than a single bone.



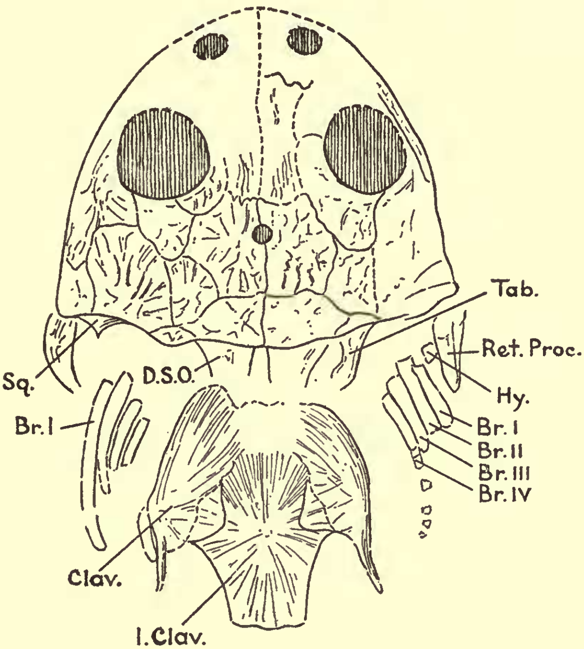
TEXT-FIG. 10.— ? *Batrachosuchus.* (D.M.S.W., B.140). $\times \frac{2}{3}$. Atlas associated with the original of Text-fig. 9. A, From below ; B, from in front ; C, from above ; D, from behind.

PELOROCEPHALUS MENDOZENSIS Cabrera

The specimen, a skeleton, was found as a weathered impression to which films of bone adhered, showing the palate and misplaced lower jaw. The palate, as Cabrera rightly recognized, is extremely like that of *Batrachosuchus*, agreeing in general proportions very closely with *B. browni* though (very probably owing to the imperfect preservation) the subtemporal fossa is rather wide. The condyles agree, and the suture bounding the parasphenoid is shown sufficiently to make it evident that the exoccipital met the pterygoid in a long suture. The lower jaw shows an anterior border to the articular facet exactly similar to that in the jaw referred above to *Batrachosuchus*, and the remains of a similar long retroarticular process. The specimen is preserved in Buenos Aires.

" PLATYCEPS " WILKINSONI Stephens

The following account is based on an enlarged photograph of the type specimen, which I actually handled about 30 years ago, (Pl. 39 and Text-fig. 11). The specimen, which extends backward to show some 25 body segments, is seen from above as dark grey crushed bone on a grey-yellow, fine-grained sandy matrix. The lower jaws are in position and the head, shown from above, is widened by being flattened almost into a plane. The skull is widest across the quadrate condyles and is semi-elliptical. The occipital border is straight and lies behind the quadrates, there being some rounding of the hinder edge of the tabular to enable it to pass directly into the hinder border of the ornamented outer surface of the squamosal. Squamosal and quadratojugal pass inward, behind the quadrate, and then backward. The jugal



TEXT-FIG. 11.—"*Platyceps*" *wilkinsoni* Stephens. × $1\frac{2}{3}$. Tracing of the skull, branchial arch skeleton and dermal shoulder girdle, made from an enlarged photograph of a specimen (the type) from Gosford, New South Wales, now in Sydney. (Compare with Plate 39). *Br.I–IV*, branchial arch skeletons I–IV; *Clav.*, clavicle; *D.S.O.*, dermosupraoccipital; *Hy.*, hyoid arch skeleton; *I.Clav.*, interclavicle; *Ret.Proc.*, retroarticular process of the lower jaw; *Sq.*, squamosal; *Tab.*, tabular occipital process.

is extremely shallow lateral to the large orbit, and the shallow maxilla stretches backward below it. The orbits are widely separated, of considerable size, but leave a relatively large preorbital face. The tabulars and dermosupraoccipitals bear powerful occipital flanges which pass backward and inward, showing that the condyles must have been placed far back, though it is evident that the dermal processes have been flattened out into the plane of the skull top and the extent of their projection back thus exaggerated. The retroarticular part of each jaw ramus is visible as a long projection.

The most striking quality is, however, the presence of long bony ceratobranchials. The ceratohyal is, perhaps, visible on each side of the head as an obscure stain mesial to the long retroarticular process, but four ceratobranchials are clearly shown on each side between this element and the outline of the body as suggested by the clavicle. Each ceratobranchial is a bony rod lying close pressed against its fellows, the anterior ends of the rods seem to lie along a line placed obliquely, its outer end further forward than its mesial point. The chief bones in all the arches are of much the same length, but it is evident on the left side that the first ceratobranchial is greatly extended by some structure—presumably cartilage—for a very long distance, whilst on the right side the last ceratobranchial has three or even more independent rings of bone surrounding its distal end, and there is a suggestion of a very extensive spread of soft structures beyond them.

The vertebral column is represented by paired series of structureless bony masses. These seem to be in general paired ossifications in the neural arches, with slight suggestions of other paired ventral bones. The ribs are short, nearly straight bones, widening proximally in a manner which suggests that they may have had double cartilaginous heads, but actually ending as bone some distance lateral of the vertebrae. The distal ends of the ribs sometimes widen, possibly as a result of crushing of a very thin bony cylinder. The first three vertebrae seem to be somewhat more massively ossified than those further back, but curiously there seem to be no ossifications in the exoccipital condyles.

The dermal shoulder girdle is well shown from above, the structure of its lower surface " printing through ". The interclavicle is large, two-thirds as long as the skull table, and its anterior end seems to have been almost semicircular, the widest point being about at mid length. From here its lateral borders pass inward and backward to end abruptly at a nearly straight transverse posterior border. The clavicles have a long overlap on the ventral surface of the antero-lateral parts of the interclavicle, and probably just meet at its anterior end. Their ventral parts are expanded, the dorsal process apparently turning a little backward and being capped by a cleithrum.

The scanty ossification of the vertebral column and the apparent lack of ossification in the exoccipitals suggest that *Platyceps* is very young, as indeed its very small size in comparison with other Brachyopids makes probable. The well ossified ceratobranchia thus imply that the animal retained its external gills into adult life, and was neotenous, as seems to have been the case in the " Plagiosaurid " *Gerrothorax*, where Nilsson (1945) has recorded the existence of ossified ceratobranchials in an obviously adult animal.

"PLAGIOSAURIDS"

Description of Material

The genus *Plagiosternum*, established by E. Fraas (1889) for fragments from the Upper Muschelkalk of Crailsheim, has had other specimens referred to it. But the skull is still represented by fragments whose areas do not overlap, so that all that can be said about it is that it may well have resembled those of *Plagiosaurus* and *Gerro-*

thorax. The skull described by Fraas (1913) as "*Plagiosternum*" *pulcherrimum* (now referred to the genus *Gerrothorax*) is the only one belonging to the group which is undistorted and really well preserved, but unfortunately the hinder surface of the quadratojugal and quadrate is broken off on the right side and completely missing on the left, and sutures are difficult to trace on the very richly ornamented outer surface. Von Huene (1922) was the first to attempt to do so. Tage Nilsson (1937) has produced another version which for the postorbital part agrees reasonably with von Huene's paper, but differs absolutely for the more anterior regions. Nilsson's account of a Swedish specimen, *Gerrothorax rhaeticus*, includes a description of a strip of the hinder part of the dorsal surface of a skull whose dorso-ventrally compressed occiput is also shown, and inspection of the material shows that his excellent figures make the structure evident. Thus we have evidence in support of Nilsson's reading of the difficult skull now in Stuttgart.

A fragment of the right hinder corner of a skull from Halberstadt, the type of Jaekel's *Plagiosaurus depressus*, is illustrated by Nilsson in an excellent photograph, and the structure of its dorsal surface is evident. It is differentiated from all others by the meeting of the dermosupraoccipital and postfrontal (!) so that the parietal does not touch the supratemporal.

The only other described genus is *Plagiosuchus* von Huene (1922). This is represented by a skull whose palate is largely shown, two misplaced lower jaws, an atlas, some ribs, a scapulocoracoid and clavicles and interclavicle, in articulation but incomplete posteriorly. There are no ways in which this specimen can be compared in detail with other Plagiosaurs, but it is important because its lower jaw has an immense retroarticular process, similar to, though proportionally longer than that which I have described above as *Batrachosuchus*. There is also an atlas, a single bone again much like the one I have referred to *Batrachosuchus*.

Points of Agreement with Older Brachyopids

Thus the Plagiosaur skull is reasonably well known: it agrees with that of the older Brachyopids in such important characters as:

(1) The way in which, as shown in *Gerrothorax rhaeticus*, *G. pulcherrimus* and *Plagiosaurus depressus*, the pretympanic flange of the squamosal wraps round the outer side of the quadrate and forms a laterally concave face on the occipital surface, ending, as far as one can judge from the somewhat damaged material, in a ridge which faces a similar border of the pterygoid, the nature of the quadrate not being clearly shown.

(2) The up-turning of the lateral wings of the pterygoids from the subtemporal fossae, so that the palate forms a broad ∩-shaped arch (seen in *G. pulcherrimus*, less well in *G. rhaeticus* and *Plagiosternum granulosum*).

(3) The fact that the occipital condyles lie far behind the dermosupraoccipital.

(4) The absence of an otic notch.

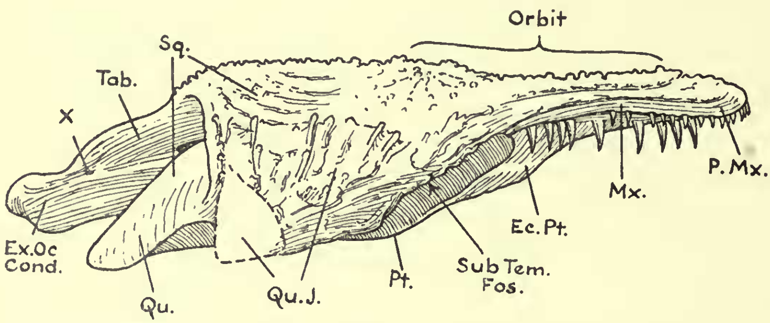
(5) The broad parabolic outline.

(6) The existence of a very large retroarticular process of the lower jaw.

(7) The extreme shallowness of the anterior part of the skull to the hinder end of the maxilla, and the deepening seen in side view, from a point behind the orbit to the quadrate condyle (cf. Text-fig. 12).

The differences in the pattern of the dermal bones of the skull roof, which distinguish the various genera, are obviously due to "improvisations" to enable a series of bones growing outward from centres more or less fixed to fill a steadily contracting area. Even in *Batrachosuchus* this difficulty is seen in the preorbital surface; in the Plagiosaurs it spreads to the temporal region.

Thus the close relationship between the Upper Permian and Lower Triassic typical Brachyopids and the Middle and Upper Triassic Plagiosaurs is obvious, depending on special detailed common peculiarities not known in any other contemporary Labyrinthodonts.



Text-fig. 12.—*Gerrothorax pulcherrimus* (Fraas). Drawn from a cast in the Museum of Zoology, Cambridge. × ⅜ approx. Lateral view of the skull based on a photograph taken at a distance of some 12 ft., and then enlarged: it is thus very nearly a parallel projection. *Ec.Pt.*, ectopterygoid; *Ex.Oc.Cond.*, exoccipital condyle; *Mx.*, maxilla; *P.Mx.*, premaxilla; *Pt.*, pterygoid; *Qu.*, quadrate; *Qu.J.*, quadratojugal; *Sq.*, squamosal; *Sub.Tem.Fos.*, arrow directed into the subtemporal fossa; *Tab.*, tabular; *X*, tenth cranial nerve foramen.

Dvinosaurus Compared with Older Brachyopids

In 1919 I suggested that the then undescribed *Dvinosaurus* from the Russian Upper Permian was a possible ancestor of the Brachyopids, pointing out (1926: 199) the existence of bony branchial arches and suggesting that the animal was neotenous. In 1936 a description of *Dvinosaurus* by P. P. Sushkin was published posthumously; this is still of great value, even though in 1938 Bystrow gave us a beautifully illustrated account and discussion of the animal. Sushkin accepted the view that *Dvinosaurus* and *Batrachosuchus* are close relatives, though demurring—obviously rightly—that, as *Dvinosaurus* is neotenous, it cannot well be an actual ancestor of the other form. He was at that time the only man who had examined both animals, and he added to the set of resemblances I had set out the remarkable similarity between the stapes of the two animals, a matter of importance, for the massive bone differs greatly from those of all other Labyrinthodonts.

Bystrow agrees that in general appearance the skull of *Dvinosaurus* resembles the Brachyopids, but finds (pp. 271, 272) a series of differences which are :

(1) *Batrachosuchus,* though very large, lacks ossified basioccipital and supra-occipital.

(2) In *Batrachosuchus* the parasphenoid and the pterygoids are united by a strongly toothed suture, whereas in *Dvinosaurus* this arrangement is lacking. If there be an attachment between these bones in *Dvinosaurus* it has no resemblance to the long " sutura paraspheno-pterygoidea " of *Batrachosuchus.*

(3) Other matters in which *Batrachosuchus* differs still more from *Dvinosaurus* are the reduction of the paroccipital, the loss of any trace of the intertemporal, the proportionately short palatal ramus of the pterygoid, and the passage of the sulcus jugalis (of the lateral line) along the squamoso-quadratojugal suture.

Most of these differences are the results of evolutionary change of characteristically labyrinthodont type, since :—

(1) All early (Lower Permian) Labyrinthodonts have a well-developed basioccipital, some few a supraoccipital, bone. All Upper Triassic Labyrinthodonts lack both bones.

(2) Several Lower Permian, and nearly all Upper Carboniferous, Labyrinthodonts have a movable articulation of the pterygoid on the basipterygoid process. All Triassic Labyrinthodonts have a long sutural attachment of the pterygoid to the parasphenoid.

(3) All Lower Permian Labyrinthodonts (except *Eobrachyops*) have an ossified paroccipital—in part visible from behind—but no Upper Triassic form retains that condition, the paroccipital ceasing to be ossified and being concealed from view by a meeting of the exoccipital and tabular. An intertemporal bone exists in Seymouriamorphs of all ages, and in many early Labyrinthodonts—for example, it is present in *Loxomma* but has been lost in all other Loxommids. Amongst Rhachitomi an intertemporal is present in the so-called Edopsids (most of which are of Pennsylvanian age) and in Romer's Trimerorhachoidea (mostly Carboniferous, with some early Permian descendants). All other Rhachitomi and Stereospondyli lack an intertemporal, obviously by loss. Thus its occurrence in *Dvinosaurus* is merely the retention of a primitive character.

By a comparison between all then-known Lower Permian and all Triassic Labyrinthodonts I showed in 1919 that a great enlargement of the interpterygoid vacuities was a characteristic change found in that group as it is traced from its beginning to its end. Thus the reduction in the length of the palatal ramus of the pterygoid in *Batrachosuchus* as compared with *Dvinosaurus* is exactly what would be expected.

The passage of the sulcus jugalis along the squamoso-quadratojugal suture in *Batrachosuchus* does not exist ; Bystrow was unfortunately misled by my published photograph.

The only other difference is that in *Dvinosaurus* the interclavicle has a long narrow posterior extension and a median incision as a long narrow slit anteriorly, whilst in " *Platyceps* " the interclavicle has a wide posterior end terminating in a gently rounded but essentially transverse border, and no indications of an anterior median slit. The clavicles of *Dvinosaurus* nearly approach one another but are narrow, whilst those of "*Platyceps*", also not in contact with one another, are greatly widened ventrally. There is thus a real difference between *Dvinosaurus* and the later forms.

But *Dvinosaurus* is neotenic: it retains a larval condition physiologically and structurally. It is true that "*Platyceps*" is larval and probably neotenic, as is *Gerrothorax*. But it is probable that the extent to which larval qualities were lost in neotenic Labyrinthodonts could vary, for metamorphosis was obviously a long process in Labyrinthodonts, for example in *Archegosaurus*, where an animal with a skull length of 7·0 cm. may still retain the denticles guarding the inner openings of the branchial clefts. Narrow lower ends to the clavicles are found in *Eryops* and in Branchiosaurs, and may well be a persistent larval feature.

Romer (1947 : 125) accepts Bystrow's view, and elaborates a comparison with *Trimerorhachis* and *Saurerpeton*. But Sushkin had, with a true instinct, recognized that in *Dvinosaurus* . . . " there is a well differentiated processus internus of the pterygoid, tapering admesially; its posterior edge being thickened and bearing a facet for the articulation with the parasphenoid; the articular surfaces of the pterygoid and parasphenoid fit completely and there is no ground for supposing that there existed also a junction of the pterygoid with a true processus of the chondrocranium which may not have been preserved in the fossil condition ". He recognized a real resemblance to *Trimerorhachis* in this matter. It is evident that the condition is unusual, the original basipterygoid process having vanished in association with a great thinning of the basisphenoid, a new articulation between membrane bones having taken its place. I can see no reason why the parasphenoid and pterygoid so brought into apposition should not later gain a sutural connection, as they did in the development of *Eryops* from an *Edops*-like ancestor where, however, the basisphenoid core of the process remains (even long after the sutural attachment of the two membrane bones has spread into a long flat sheet) as the cartilaginous infilling of the " conical recess ". Thus this character is no evidence against a close association between *Dvinosaurus* and the Brachyopids.

I would add to the features in which *Dvinosaurus* resembles the Brachyopids the fact, shown in the two side views of the skull and lower jaw published by Sushkin (1936 : 60, fig. 4) and Watson (1951 : 102, fig. 42), that the face is very shallow, the temporal region relatively deep.

EOBRACHYOPS TOWNENDAE **gen. et sp. nov.**

Description of Material and Manner of Fossilization

Some twenty-five years ago I found, in the mass of unattractive, unregistered Texan Permian material belonging to the Cope collection in the American Museum of Natural History, a small Labyrinthodont skull almost entirely covered by a most unpromising matrix. This was mainly a very hard, dark red, cemented mudstone, partly represented by spheroidal nodules and for the rest by the light green matrix in which bone structure is usually destroyed. This specimen I prepared with a hammer and needle-pointed chisels in odd hours during the early part of the late war when I was fully engaged in government work. The preparation is satisfactory, such matters as the surface ornament and sutures on the outer surface being perfectly shown. But the specimen has been damaged, and it is necessary to explain its condition in some detail to justify the restored drawings which I now publish, and to bring out its eventful history, which has a bearing on the mode of deposit of the rocks in which it was buried.

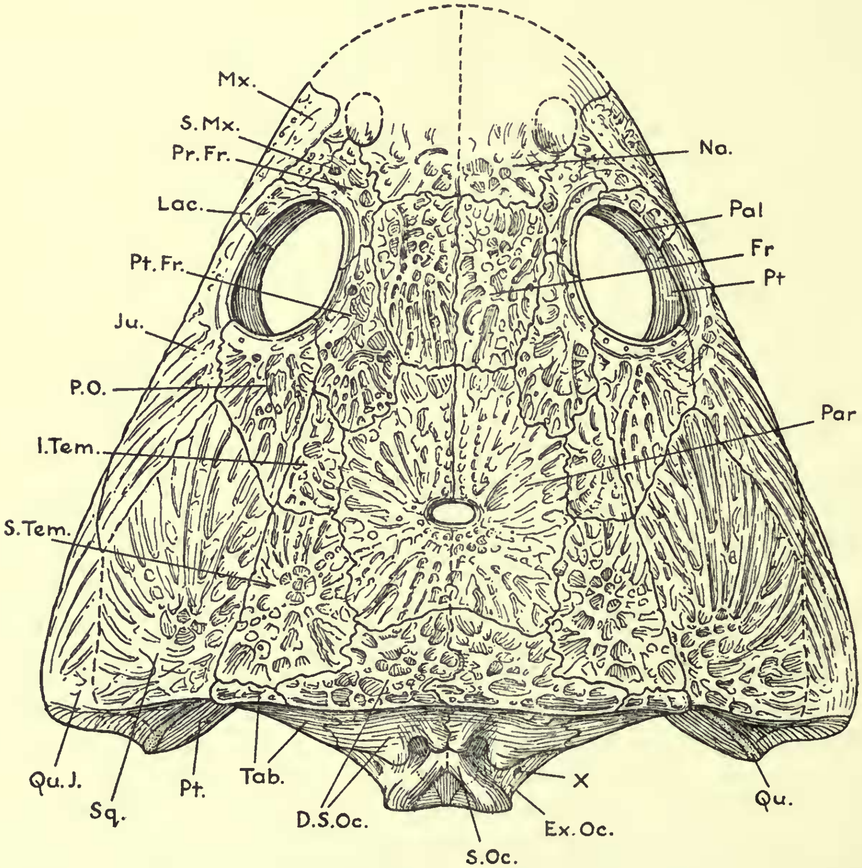
The skull, very shallow in front, is deep in the occipital region. The extreme end of the nose, and part of the anterior surroundings of the left orbit, had been broken off and lost before collection, and the right quadrate region is weathered away. The animal after death was disturbed ; the left squamosal turned outward into the plane of the upper surface, the left pterygoid disarticulated and carried over to the right side of the palate. It now rests on the ventral surface of the right clavicle, which has moved forward so that its dorsal ramus passes up through the right interpterygoid vacuity to the roof of the skull. The left ramus of the lower jaw is misplaced so that its inner surface faces upward, lying below, and separated by some 5–10 mm. from, the visceral surface of the left squamosal. The anterior part of the jaw was not collected. Below this jaw lies the interclavicle with its anterior end forward. On the ventral side of this bone lie a number of vertebral elements, whilst the ventral surface of the right clavicle is underlain by some ribs and a number of dermal scales, of which others are to be found elsewhere. Such disturbance seems to me of a kind which might have been brought about by pulls given by small animals at a time when a good deal of the skin and other soft parts were still present, and the whole appearance is more consistent with a drying carcass than with one under water.

After these displacements the skull was fractured, two cracks crossing the table from side to side, the central strip so separated being depressed 2–3 mm. below its surroundings. At the same time the upper end of the dorsal ramus of the clavicle was forced through a parietal, the fragments so formed standing up round its tip like a tent, and the exoccipitals were fractured and forced up relative to the descending flanges of the dermosupraoccipitals. It is obvious that these fractures can only have been made by pressure exerted by a heavy soft body into which the tent of parietal fragments, still held together by skin, could have been forced. And the only such structure I can think of is the foot of a large animal : and an animal foot could only exert sufficient pressure in air.

Despite this damage it is possible to make reconstructions which must be nearly accurate, as the right squamosal is in its natural position, though the quadratojugal has been forced upward within it and has lost its lower margin. The orbital part of the skull is extremely flattened in the actual specimen, but seems to retain very nearly its original shape. The extreme depth of the cheek at the quadrate was suggested by continuing the anterior part of the border of the quadratojugal backward, and estimating the place of origin of the surface ornament of that bone from the radial arrangement of its surviving parts. The point so determined is confirmed because it enables a drawing of the lower jaw (previously made in what appeared to be a natural position) to have an obviously natural occlusion when placed in articulation with the inferred quadrate condyle. The reconstructions were made by Miss J. Townend after we had agreed on all matters of detail.

Skull Roof

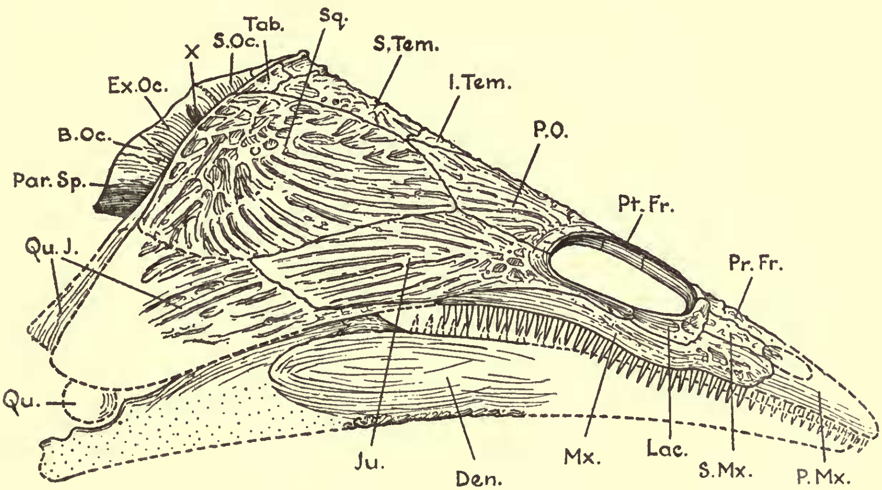
The remarkable features of the skull roof are the small size, wide separation, and very anterior position of the orbits, and the absence of an otic notch. All the bones of a normal Labyrinthodont skull roof are present, those which build up the " table " covering a very unusually large part of the whole area.



Text-fig. 13.—*Eobrachyops townendae* gen. et sp. nov. Reconstruction of the type specimen (A.M.N.H. 2455). $\times 1\frac{1}{3}$. Dorsal aspect of the skull, viewed at right angles to its upper surface. *D.S.Oc.*, dermosupraoccipital ; *Ex.Oc.*, exoccipital ; *Fr.*, frontal ; *I.Tem.*, intertemporal ; *Ju.*, jugal ; *Lac.*, lachrymal ; *Mx.*, maxilla ; *Na.*, nasal ; *P.O.*, postorbital ; *Pal.*, palatine ; *Par.*, parietal ; *Pr.Fr.*, prefrontal ; *Pt.*, pterygoid ; *Pt.Fr.*, postfrontal ; *Qu.*, quadrate ; *Qu.J.*, quadratojugal ; *S.Mx.*, septomaxilla ; *S.Oc.*, supraoccipital ; *S.Tem.*, supratemporal ; *Sq.*, squamosal ; *Tab.*, tabular ; *X*, tenth cranial nerve foramen.

The large parietals surround a transversely widened pineal foramen, meet the frontals anteriorly, and are bordered laterally by the postfrontals, intertemporals and supratemporals. Posteriorly they are attached to the dermosupraoccipitals which stretch outwards behind the supratemporals to sutures with the small tabulars. The presence and relations of the intertemporal are quite certainly shown ; it lies between the parietal, postfrontal, postorbital and supratemporal—the position it holds in all those Labyrinthodonts in which its occurrence has been described.

The squamosal is a remarkable bone, standing nearly vertically on the side of the skull, articulating above by a long straight suture with the supratemporal and tabular with its anterior end wedged in between the long postorbital and the jugal, with which it has a very long suture. The upper part of the hinder border of the bone is narrow and is separated by a now empty space from the upper part of the posterior

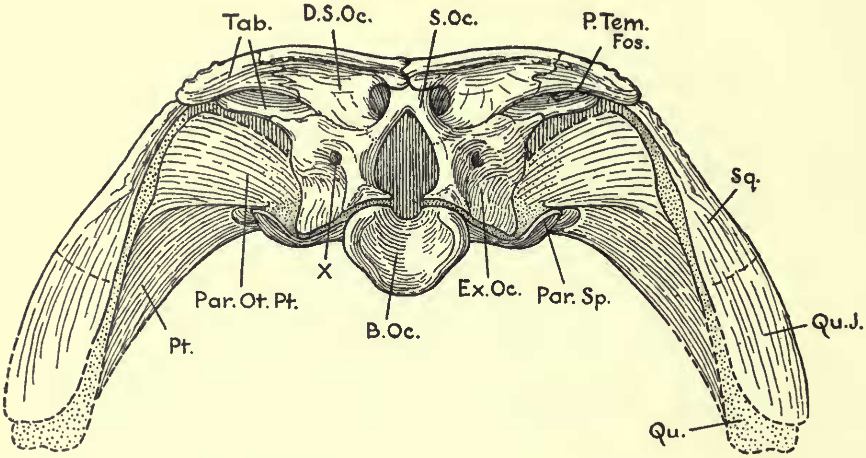


TEXT-FIG. 14.—*Eobrachyops townendae.* × 1½. Lateral aspect of the skull and lower jaw. Reference letters as before with : *B.Oc.*, basioccipital ; *Den.*, dentary ; *P.Mx.*, premaxilla.

margin of the quadrate ramus of the pterygoid. Ventrally the hinder edge of the squamosal is turned (over a rounded surface) abruptly inward nearly at right angles to its outer surface and extends inwards toward, though it does not come into contact with, the lower part of the hinder border of the pterygoid. The inner border of this part of the squamosal is turned backward, no doubt applied to a narrow ridge of the cartilaginous quadrate whose other surface was coated by the pterygoid.

The arrangement of the bones surrounding the orbit is shown with certainty. There is a large postfrontal, articulating with the postorbital, intertemporal, parietal and frontal bones, which ends anteriorly at a suture with the prefrontal. The prefrontal is attached by its inner border to the frontal and nasal, and most unusually extends forward to form part of the border of the nostril. The posterior part of the lateral border is in contact with the lachrymal, the remainder with a bone whose nature has to be discussed. This bone is excluded from the orbital margin, its posterior end being attached to that upstanding process of the lachrymal which reaches the prefrontal. From here forward to the nostril the bone is held between the prefrontal and the maxilla, its anterior border forming a good deal of the margin of the nostril. Except for a very remote possibility that the lachrymal may only be a broken anterior part of the jugal, the neighbours of this puzzling bone are certainly determined, and the only homologue which can be found for it is the septomaxilla, which sometimes has a superficial exposure.

The lachrymal is a small bone forming the anterior and lower corner of the orbital border. It is a little misplaced, but a notch bounded by the prefrontal and septo-



TEXT-FIG. 15.—*Eobrachyops townendae.* × 1⅓. Occipital aspect of skull viewed parallel to the dorsal surface. Reference letters as before with : *P.Tem.Fos.*, post-temporal fossa ; *Par.Ot.Pt.*, parotic flange of pterygoid ; *Par.Sp.*, parasphenoid ; *X*, foramen for the tenth cranial nerve.

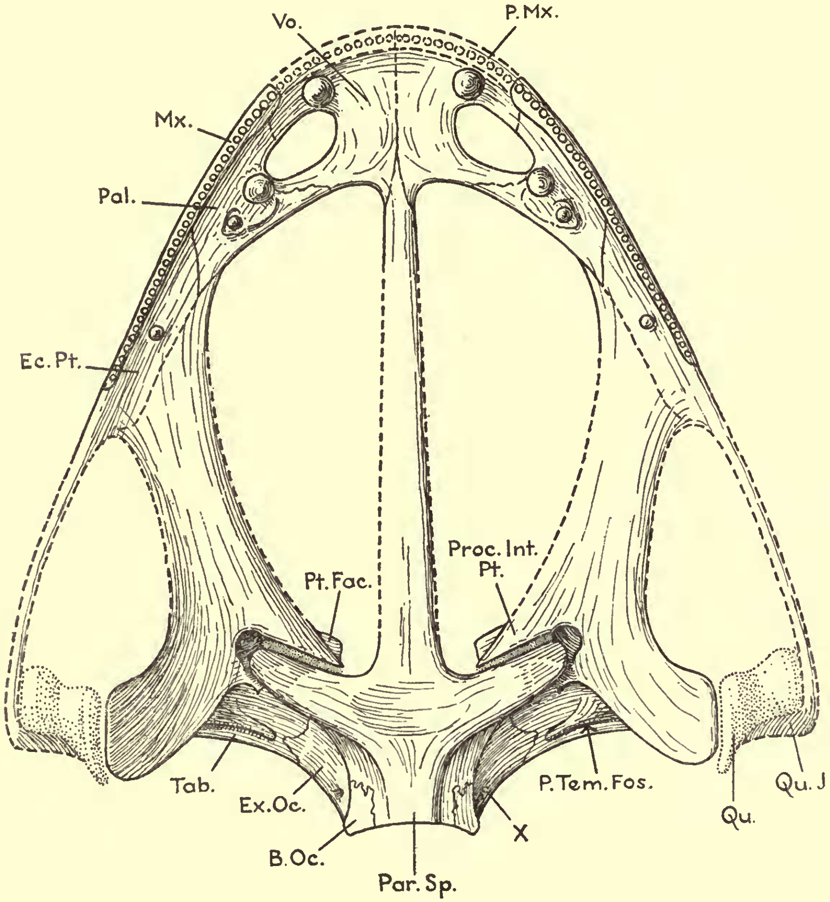
maxilla shows its original position, and the mode by which it articulates with the upper surface of the maxilla is obvious. The bone turns inward to form a wide wall to the orbit, and is apparently fused with the upper surface of the palatine bone.

The jugal forms the posterior and lower corner of the orbit, meeting the lachrymal in a suture which has been pulled apart so that the depressed surface, with an abrupt posterior ending which housed the hinder end of the lachrymal, is very clearly seen. Behind the orbit the jugal continues backward, between the postorbital and squamosal above, and the maxilla below, until it reaches the incompletely preserved quadratojugal.

The quadratojugal has a long exposure on the lateral surface of the skull, then turns in to continue downward the posterior surface of the squamosal.

Occiput

One of the more remarkable features of this skull is the amount by which the occiput extends behind the posterior border of the ornamented table. In consequence the occipital flanges of the dermosupraoccipitals are largely visible from above as a wide



Text-fig. 16.—*Eobrachyops townendae.* × $1\frac{1}{3}$. The palate viewed at right angles to the parasphenoid. Reference letters as before with : *Ec.Pt.*, ectopterygoid ; *Par.Sp.*, parasphenoid ; *Proc.Int.Pt.*, processus internus of the pterygoid ; *Pt.Fac.*, dorsally placed process of the pterygoid perhaps for the epipterygoid ; *Vo.*, vomer.

triangle with a truncated apex. These flanges are marked off by a transverse groove lying below and behind the rounded ridge, which is the hinder border of the table. Each flange is notched posteriorly by a groove which passes forward near the middle line below the skull roof. The lateral borders of the flanges stand out freely above the post-temporal fossae.

The tabular has a very slender occipital flange, not visible from above, which stretches inward and downward behind the cartilaginous paroccipital.

In occipital view the basioccipital forms a large, concave condyle, the " articular " surface being spheroidal, though notched on its upper surface for the notochord. The lateral borders are rounded and thickened. The upper surface is largely covered by the lower ends of the exoccipitals, which send inward flanges (which probably did not meet) below the foramen magnum. The exoccipitals then rise as columns on each side of the foramen magnum, approaching one another until they are broken across and now show a damaged upper surface. Their apparent continuation over the summit of the foramen magnum is by a small bone (or bones) which is notched below, and extends down the sides of that opening so as to meet them with a continuous admesial surface, there being no trace of the step which in most Labyrinthodonts receives a cartilaginous supraoccipital. It is therefore likely that the bone in question is actually a supraoccipital. From its posterior surface each exoccipital extends forward and outward, surrounding the vagal foramen, and is perforated by two more ventrally placed small openings which (by comparison with *Capitosaurus*) may be for the XIIth cranial nerve. The rest of the bone clearly sheathed the posterior surface of the persistently cartilaginous paroccipital, whose position is fixed by that of the occipital flange of the tabular, which laterally sheathed its posterior face.

Palate

The parasphenoid is a remarkably large and elaborate bone. Its hinder margin reaches the rim of the single concave occipital condyle, and indeed appears to border the whole lower half of this structure, surrounding and hiding the basioccipital in ventral view. Laterally the parasphenoid ends in a suture with the exposed lateral surface of the basioccipital, but further forward this suture rises to cut the surface to which the ventral face of the exoccipital is attached. From this place the parasphenoid widens, its border passing outward and forward to help to form an immense basipterygoid process. In this region the bone is very shallowly concave midventrally, but then rises a little so that the anterior face of the process becomes a deep and apparently vertical, transversely placed articular surface, which is applied to a corresponding facet on the pterygoid. Mesial of this articulation the border of the parasphenoid passes inward round the interpterygoid vacuity to extend anteriorly as the outer edge of a processus cultriformis. The bone is then concealed by matrix until what appears to be the ventral surface of its anterior end is exposed at the anterior end of the specimen. The parasphenoid behind the basipterygoid process has a nearly flat central region bounded on each side by a depressed area for attachment of recti capitis muscles over the lateral parts of the basioccipital.

The pterygoid bears a powerful " internal process " which passes inward from the meeting point of the palatal and quadrate rami. The straight borders of this process meet at a point directed mesially at the hindmost place on the border of the interpterygoid vacuity. This process is obliquely truncated by an apparently flat articular surface opposed to the corresponding face of the parasphenoid ; the two are separated in the specimen by a film of matrix about one millimetre thick. The front face of the articular process of the pterygoid is obviously continued outward and forward as the lateral margin of the interpterygoid vacuity. Lateral to and immediately behind the articular face the lower surface of the pterygoid is excavated by a smoothly rounded pit, which lies immediately lateral to the tip of the parasphenoid. The floor of this pit extends inward onto a thin shelf of bone separated, in the specimen, from the parasphenoid by about 2 mm. of matrix. It is in every way probable that this space was originally occupied by a cartilaginous basipterygoid process of the basisphenoid. Laterally the pterygoid turns down to form the border of the subtemporal fossa, and, with the much deeper surface of the quadrate ramus, makes a sheath to the temporal muscles, and bounds the characteristic U-shaped section of the palate.

Further back the short quadrate ramus of the pterygoid is abruptly produced downward as a deep flat sheet of bone with nearly parallel anterior and posterior edges. The posterior border, originally applied to a cartilaginous quadrate, lies along the hinder and inner border of the squamosal, but is throughout separated from it by a narrow space originally filled by the quadrate. Above the level of the inwardly directed shelf, which lies above the presumed cartilaginous basisphenoid, the parotic plate of the pterygoid rises vertically to, or very nearly to, the skull roof. The anterior end of this part of the ramus plunges into matrix.

The only other visible feature of the pterygoid is a small triangular shelf extending forward into the back of the interpterygoid vacuity from the anterior face of the articular process. This has a flat ventral surface, and lies high in the skull, presumably about at the level of the upper surface of the cartilaginous basisphenoid in its vicinity. It may have supported the foot of an epipterygoid.

No part of the palatal ramus of the pterygoid is exposed except for its anterior tip, seen through the orbit, which is grooved for attachment to the ectopterygoid and palatine. The ectopterygoid is only represented by a single large tusk, whose length is completely preserved.

The palatine bone is well shown. Its lateral border is throughout in contact with the inner surface of the maxilla, and its inner margin—forming part of the border of the interpterygoid vacuity—is completely visible. At its contact with the ectopterygoid the palatal exposure of the bone is extremely narrow. Anteriorly, at the level of the forward end of the vacuity, the bone bears two very large teeth; the anterior of these is a mature tooth of circular section, the tip being lost, the posterior was in process of growth, arising within a ring of bone standing out from the palatine. The crown of this tooth lies misplaced nearly horizontally and is sharp-pointed, of circular section, and longitudinally striated. Mesial of these teeth the bone extends inward, with a narrow exposure between the nostril and the vacuity, to reach and be overlapped by the vomer. Anteriorly to the teeth the palatine stretches forward internally to the maxilla until it meets the vomer, excluding the maxilla from the internal nostril.

The vomer is a large bone well shown on the right side of the specimen. Its contacts with the palatine have just been described; it forms part of the border of the interpterygoid vacuity, and has a process which extends backward along the lower surface of the parasphenoid. It bears one large tooth, of which only half the root is preserved.

The premaxillae have been broken away, but a small process of one of them, resting on the upper surface of the vomer, can be seen through the right external nostril.

The maxilla is a very shallow bone deepened anteriorly where it is attached to the septomaxilla. It ends anteriorly in an almost vertical suture with the premaxilla. Its lower border turns a little down posteriorly. It bears a series of small close-set teeth, apparently uniform and circular in section, sharp-pointed and unexpectedly high at the hinder end of the row.

Lateral Line

Lateral line grooves are very poorly represented. There is a somewhat unusual groove which nearly surrounds the orbit. It begins about at the suture between the prefrontal and lachrymal, and passes over the pre- and postfrontals and the post-orbital on to the jugal, along which it passes—apparently just touching the lachrymal and then descending on to the maxilla. There is a possible short branch crossing the postorbital towards the intertemporal. The rest of the skull and the lower jaw seem to lack any trace of these structures.

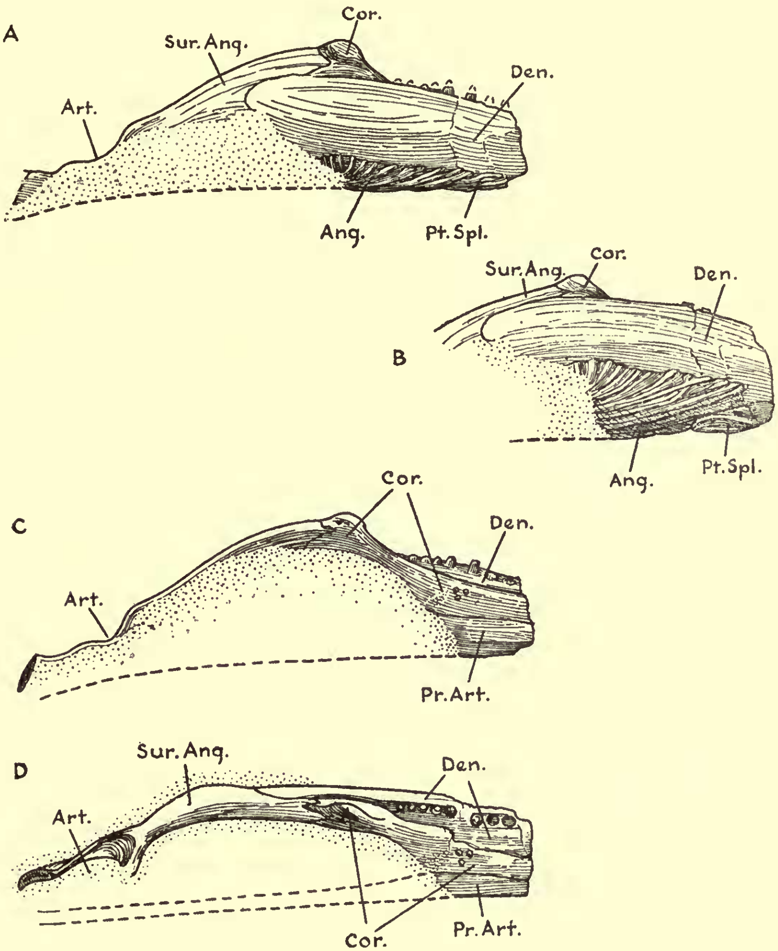
Lower Jaw

The hinder part of the left lower jaw is preserved, but is largely concealed by irremovable matrix. It is of normal Labyrinthodont structure, but possesses some unusual features. There is every reason to believe that its lower border was straight; there is a relatively long retroarticular process, a marked coronoid process, and a lightly ossified articular. The angular is the usual boat-shaped bone with a radiating ornament of ridges, and the hinder end of what is presumably the postsplenial is similarly ridged. Little but the upper border of the surangular is exposed. This bone extends back along the outer surface of the retroarticular process, in front of which its upper edge bears a rounded notch marking the position of the articular surface. From the anterior end of this notch a process passes inward, which laterally carries a small part of the articulation for the quadrate, whilst mesially it seems to have sheathed the front of the partly cartilaginous articular. The upper border of the bone outside the supra-meckelian fossa is thick and rounded, ending at a clearly marked suture with that hinder end of the coronoid which forms a definite process with a narrow but rounded summit. The outer surface of the surangular has no ornament so far as can be seen, and the dentary overlaps it.

The dentary reaches the ornamented surface of the angular and the postsplenial. Its outer surface is rounded from dorsal to ventral edges, and is perfectly smooth. The narrow dentigerous border supports a single row of small, close-set teeth of circular section. Anteriorly a smooth surface of the dentary lies above the coronoid on the inner surface.

The coronoid is applied to the inner surface of the dentary, rising to its process, where it is wedged into the surangular. It surrounds the anterior end of the supra-meckelian fossa and stretches forward on the inner surface of the jaw as far as the specimen extends. This surface bears a patch of three small hemispherical denticles, but is otherwise smooth. Its lower border rests on the prearticular.

The prearticular is represented by a section of its hinder end separated by a space (which represents the cartilaginous articular) from the retroarticular part of the surangular. Anteriorly its lower margin is overlapped by the postsplenial.



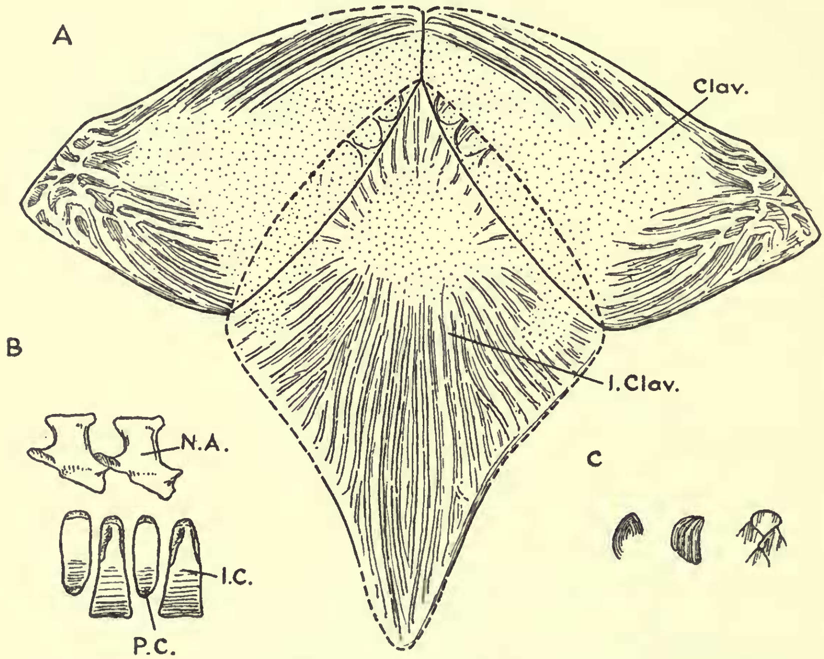
TEXT-FIG. 17.—*Eobrachyops townendae.* × $1\frac{1}{3}$. The hinder part of the lower jaw. A, Right side, external aspect; B, right side viewed somewhat from below; C, left side, from within; D, left side from above. *Ang.*, angular; *Art.*, articular; *Cor.*, coronoid; *Den.*, dentary; *Pr.Art.*, prearticular; *Pt.Spl.*, post splenial; *Sur.Ang.*, surangular..

The very much bowed upper edge of the lower jaw makes it difficult to determine its relation to the skull. It seems, however, clear that the jaw was so placed that the lower border was turned in, the flat inner surface facing partly upward. Such a position brings the upper part of the outer surface of the dentary (below its tooth bearing edge) vertical, as it should be, and places the little of the articular cavity that can be seen in a reasonable position.

Vertebral Column

The vertebral column is represented by a single neural arch and a number of "central" bones. All these are fractured and incomplete, but, so far as they go, are well preserved.

The neural arch seems not to have been co-ossified with its fellow of the other side; it has a considerable neural spine expanded fore and aft at its summit. This spine arises from an elongated body, along the side of the neural canal, bearing narrow pre- and postzygapophyses which have no special character. The lower border of the bone is broken and does not show the way in which it articulated with the central elements. There is, however, a short, anteriorly placed transverse process.



Text-fig. 18.—*Eobrachyops townendae.* × $1\frac{1}{3}$. A, Reconstruction of the dermal shoulder girdle from below. Areas in which the ornament is represented are seen on one side or the other, borders in broken line restored, dotted area has not been seen on either side, being hidden by matrix or other bones (its shape has no significance). B, Reconstruction of two vertebrae from the right side; C, various scales. *I.C.*, intercentrum; *N.A.*, neural arch; *P.C.*, pleurocentrum; *Clav.*, clavicle; *I. Clav.*, interclavicle.

There are about a dozen incomplete circum-notochordal bones, all so much alike that I have been unable to distinguish intercentra from pleurocentra with certainty. They clearly surrounded a large notochord of the order of 8 mm. in diameter, their outer surface being composed of dense bone with a good surface which tends to be turned a little outward anteriorly and posteriorly. The bone is thin, about 1 mm.

thick, and the inner surface is slightly roughened and not covered with dense periosteal bone. All the fragments which show a natural termination end in a rounded point extending beyond the periosteal outer surface. Those bones which I regard as intercentra narrow dorsally from a maximum of 4·5 mm. to some 2 mm. in a height of 8·0 mm. In all cases the wide ventral end is a fracture, and it seems probable that the bones were really large segments of a cylinder and were not paired. These bones show a narrow but rather deep flattening on the posterior part of the upper end of their outer surface, which is presumably a rib-facet.

One bone, which seems to be complete, is 8 mm. high and has a maximum width of 2·5 mm. It is seen from its inner surface and is presumably a pleurocentrum. In Text-fig. 18 I have made a restoration of two vertebrae on the basis of the remains described above, and it may be mentioned as a point in its favour that it fits the occipital condyle.

Shoulder Girdle

The interclavicle and right clavicle are nearly complete, but are in part hidden by matrix. The area of the ventral surface of the interclavicle on which ornament is shown in Text-fig. 18 is exhibited on one or other side of the specimen, and its middle line is fixed by a marked median ridge on the visceral surface of its anterior end. Occasional short lengths of genuine margin, or of the overlap surface for the clavicle, fix its shape within narrow limits. The right clavicle, seen from its ventral surface, is very nearly complete, but much of it is covered by matrix and other bones.

Thus the restoration rests on adequate evidence, and it seems to be certain that the clavicles must have met for a considerable distance in front of the interclavicle. It will be noted that the total width fits neatly that of the skull. The height and direction, though not the structure of the dorsal process of the clavicle, is known; it stands up at right angles to the ventral surface of the bone and is 22 mm. high, leaving room in the body for a cleithrum of normal proportions.

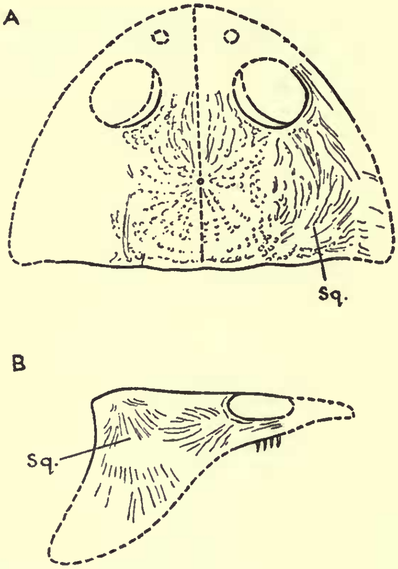
Scales

In a number of places groups of small, oval, ? bony scales may be seen (Text-fig. 18). Each has an ornament of low concentric ridges. They appear to have overlapped extensively, and are about 3 mm. across, but very thin.

Possible Relationship to Acheloma casei and Trimerorhachis

The only animal to which the Labyrinthodont described above has any similarity is that described by Broili in 1913 as "*Acheloma*" *casei*. The two specimens agree in that they have a truncated posterior border to the dermal skull, with no trace of an otic notch. In both the orbits lie far forward, with a well marked smooth border surrounding each, and are not exceptionally close together. Broili's lateral view seems to show a tooth-bearing fragment of maxilla not far below the orbit, and shows that the cheek was deep. Indeed the two skulls not only resemble one another in general shape, but in the character of their ornament and the general direction of the ridges on the cheek bones which form it. They may well belong to the same genus.

But they are specifically different. The new skull has a large, transversely widened pineal foramen, "*Acheloma*" *casei* a very small one. The table of the new skull is broader than it is in Broili's specimen, and so is the interorbital space, whilst the orbit of "*Acheloma*" *casei* is wider than that of the new form. The squamosal in "*Acheloma*" *casei* appears to be deeper than that of my animal, and the new



TEXT-FIG. 19.—*Eobrachyops casei* (Broili). × ⅔. Reconstruction of the skull drawn from Broili's figures, left side copied from right. The outline of the cheek in B, hypothetical, is based on a comparison of the ornament shown on it with that of *E. townendae*. A, Dorsal surface ; B, right lateral surface. *Sq.*, squamosal.

skull being only some twenty-five per cent larger than the old, it is impossible to explain the visible differences in proportion as due to growth. I propose to call the new specimen *Eobrachyops townendae* gen. et sp. nov. *Eobrachyops* expresses my opinion of its systematic position, *townendae* is in honour of Miss Joyce Townend, who made the drawings which illustrate this and all my other recent work. "*Acheloma*" *casei* Broili becomes *Eobrachyops casei.*

Eobrachyops comes from an unknown locality and horizon but belongs to the Cope collection, much of which came from the Wichita formation, though some is Clear Fork. Professor A. S. Romer has examined the specimen of *E. townendae* and tells me that the matrix is certainly Clear Fork, as is *E. casei* It now bears the number Amer. Mus. 2455.

The only contemporary form which resembles it at all is *Trimerorhachis.*

Trimerorhachis has been described by Cope, Broili, Case, Broom and Williston, but still needs much further description. I therefore give a further account of the basicranial and otic regions.

The two genera have in common: a skull which is depressed, at any rate anteriorly, anteriorly placed orbits, an intertemporal bone in the table, a shallow (or absent) otic notch, an occipital condyle, the greater part of which is made by the basioccipital —so that it is deep and has a concave articular face—and a "movable" articulation between the basipterygoid process of the parasphenoid and the pterygoid.

TRIMERORHACHIS

Variation of Specimens

The following account is founded on four specimens which Professor Romer was good enough to send me (M.C.Z. 1169, 1975 A, B & C); and on B.M.N.H., R.576, which reached the Museum in 1885, from the collection of Waldemar Kowalevski, to whom it had been given by E. D. Cope before 1883 (as is recorded in a letter dated 30.vii.1885 from Cope to Henry Woodward in the archives of the Geology Department of the British Museum).

The skull of *Trimerorhachis* is generally believed to have been very much flattened, as much so perhaps as in a late Triassic Stereospondyl. But it seems certain that this flattening, in some cases at any rate, did not extend to the occiput, although it did to the quadrate regions of the skull.

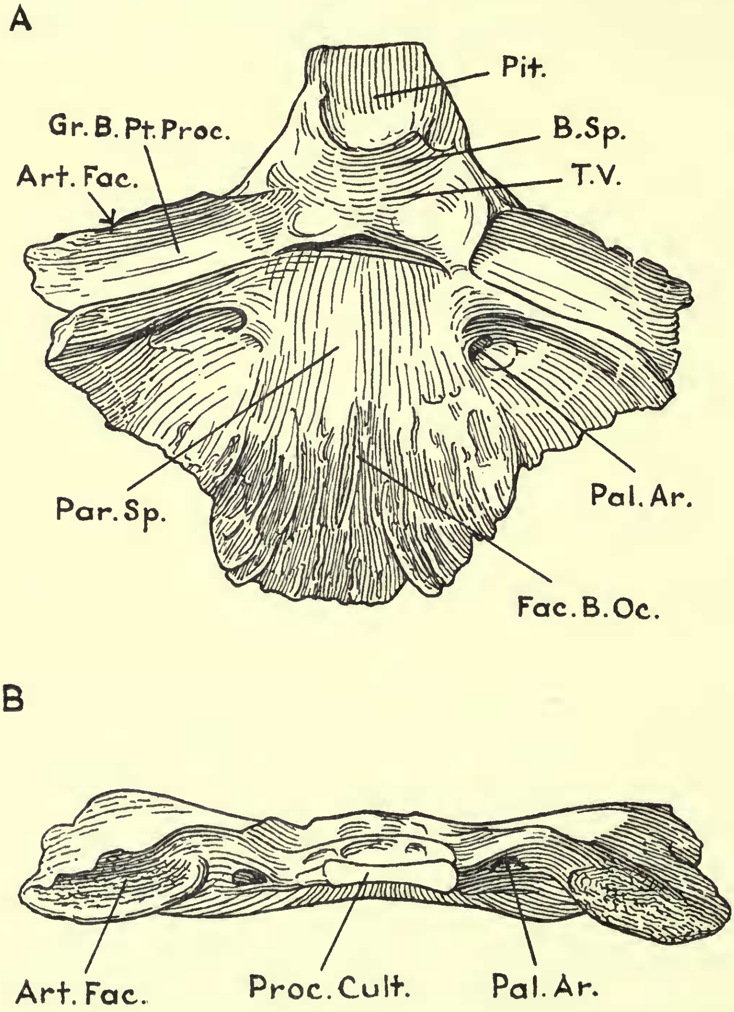
The occipital condyle is always single, and concave, but it varies a good deal in shape in different specimens—perhaps from different horizons. In one specimen before me it measures 2·3 cm. transversely, and is 1·75 cm. high. Another is 2·25 by 1·5 cm., the outline being convex throughout. Another is 2·1 by 1·6 cm. and has concave lateral borders below the middle of its height, whilst R.576 is 2·1 cm. wide and only 1·2 cm. high, the basioccipital part of the structure being greatly reduced. These variations are obviously related to the general flattening which takes place with time in Labyrinthodonts. Associated with them is a change in the height of the exoccipital above its condylar portion. In the second of the above specimens the height is 1·3 cm., in the third 1·2 cm., and in the fourth only 0·75 cm., in other words the flattening is general.

One of the specimens mentioned above (M.C.Z. 1169) has the table of the skull well preserved and visible from both upper and lower surfaces and from the back. The dermosupraoccipital bears a very obvious occipital flange 1·05 cm. deep, and this "flange" is merely the occipital exposure of a thick mass of bone whose lower surface, which lies nearly horizontally, extends forward for nearly a centimetre and obviously rested directly on the upper end of cartilaginous continuations of the exoccipital, and the paroccipital. There is no evidence of any overlap of the dermo-supraoccipital on the occipital surface of the exoccipital. Thus the minimum height of the occiput is 1·6 (condyle) + 1·2 (exoccipital) + 1·05 (postparietal flange) = 3·85 cm. (assuming—as we justifiably may—that it was vertical) and the width of the table between the otic notches directly measured is 6·3 cm., i.e. as 1 : 1·64.

Eryops in Sawin's figure is 1 : 2·43. In fact the occiput of *Trimerorhachis* is deeper and narrower than that of *Eryops* and even of *Edops*.

Brain-case

The basioccipital is a wedge-shaped bone forming the lower part of the single occipital condyle. It has a short, free ventral surface posteriorly which extends



Text-fig. 20.—*Trimerorhachis* sp. (M.C.Z., 1975). × 2. Posterior part of the parasphenoid, with co-ossified basisphenoid. A, From above; B, from in front. *Art.Fac.*, articular face on the parasphenoid for the processus internus of the pterygoid; *B.Sp.*, basisphenoid; *Fac.B.Oc.*, ridged face for attachment of the basioccipital; *Gr.B.Pt.Proc.*, groove for the cartilaginous basipterygoid process; *Pal.Ar.*, foramen for the palatine artery; *Par.Sp.*, parasphenoid; *Pit.*, depression for the pituitary body; *Proc.Cult.*, processus cultriformis of the parasphenoid cut across; *T.V.*, transverse vein.

outward to smooth lateral surfaces, usually concave, which terminate dorsally at the attachment of the exoccipital. The greater part of the ventral surface is ridged for the overlap of the hinder part of the parasphenoid, which turns upward round the bone to continue its concave lateral faces forward over a suture, so forming a deep pocket, presumably for the attachment of a recti capitis muscle. The dorsal surface of the basioccipital has a median groove for the notochord, lateral to which lie the facets for the exoccipitals, whilst anteriorly the bone thins until it gradually fades away into the upper surface of the parasphenoid.

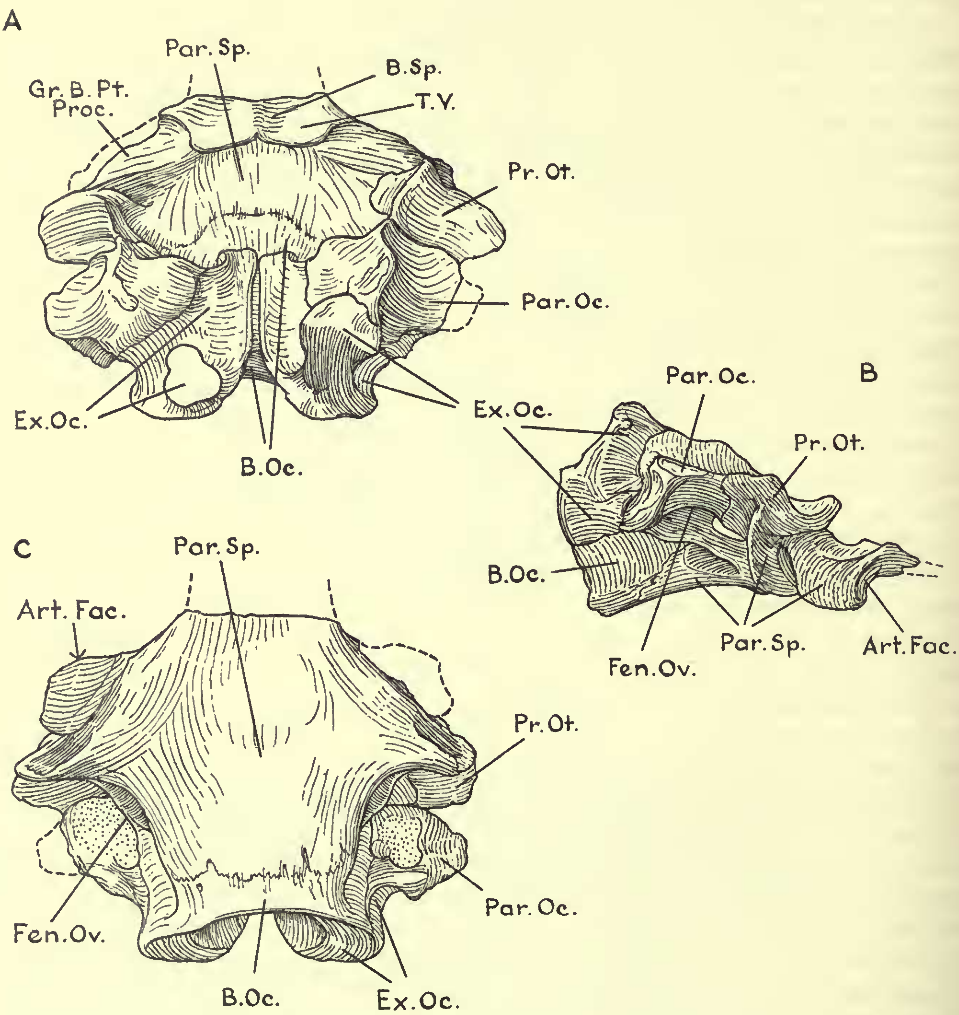
The parasphenoid is directly comparable with that of *Eryops* or—perhaps more easily—a primitive Neorhachitome. It varies a good deal in shape in different individuals, but these changes merely overlie a fundamental uniformity. On its upper surface the parasphenoid at the root of the processus cultriformis is co-ossified with an extremely thin basisphenoid. No dividing line between the two bones can be seen in section, but that the basisphenoid does indeed exist is shown by surfaces belonging to it not covered by perichondral bone, but formerly continued by cartilage. These exist posteriorly toward the basioccipital, and laterally at the base of the grooves, lying on the upper surface of the articular process, and bounded behind by the lateral ridge, which show the position of cartilaginous basipterygoid processes. Consideration of the facet on the pterygoid for these processes suggests that the cartilage was shallow, the functional articulation being between the parasphenoid and the pterygoid.

The dorsal surface of the body of the basisphenoid has a shallow concavity bounded by a transverse ridge behind, which agrees with a similar structure in *Eryops*, on whose floor Sawin held that the recti muscles had their origin. Further forward on the upper surface, at the root of the processus cultriformis, lies a depression for the pituitary, as in *Eryops*. Behind the lateral ridge on the upper surface of the parasphenoid is a smooth depression, passing out laterally, which no doubt sheathed the lower part of the proötic. In one specimen (but not in R.576) a small foramen enters the bone from the admesial end of this hollow.

The exoccipital has a base which is closely attached to, and ultimately fuses with, the upper surface of the basioccipital. This base is moulded on the upper surface of the notochord, its posterior surface forming part of the great concave " condyle ". It expands inward to floor the brain cavity and nearly (or quite) meets its fellow in the middle line. The base extends forward and a little outward until it ends abruptly at a face presumably lying in contact with the lower cartilaginous portion of the paroccipital. Anteriorly the upper surface of the base forms the floor of the vagal foramen, whose posterior wall is the massive ascending part of the exoccipital which bounds the foramen magnum. It is important to note the complete absence in *Trimerorhachis* of that perichondral extension of the exoccipital, which in *Eryops* and all its successors overlaps the paroccipital to an ever-increasing extent. The hinder surface of the exoccipital which rises to the dermosupraoccipital is essentially flat, but it bears a small protuberence a little above the level of the floor of the foramen magnum. This recalls the facet for attachment of a proatlas in many reptiles and may have had this function, for processes for the attachment of such a bone exist on the anterior faces of the atlantal neural arches (Cope & Matthew, 1915, pl. 8, fig. 1b).

The upper end of the exoccipital is abruptly truncated and no doubt continued by cartilage.

The paroccipital is well shown in three of my specimens. It is a large bone with the posterior surface covered by a smooth perichondral layer. The admesial part of its posterior surface forms a stout pillar, ending below in a rounded and laterally



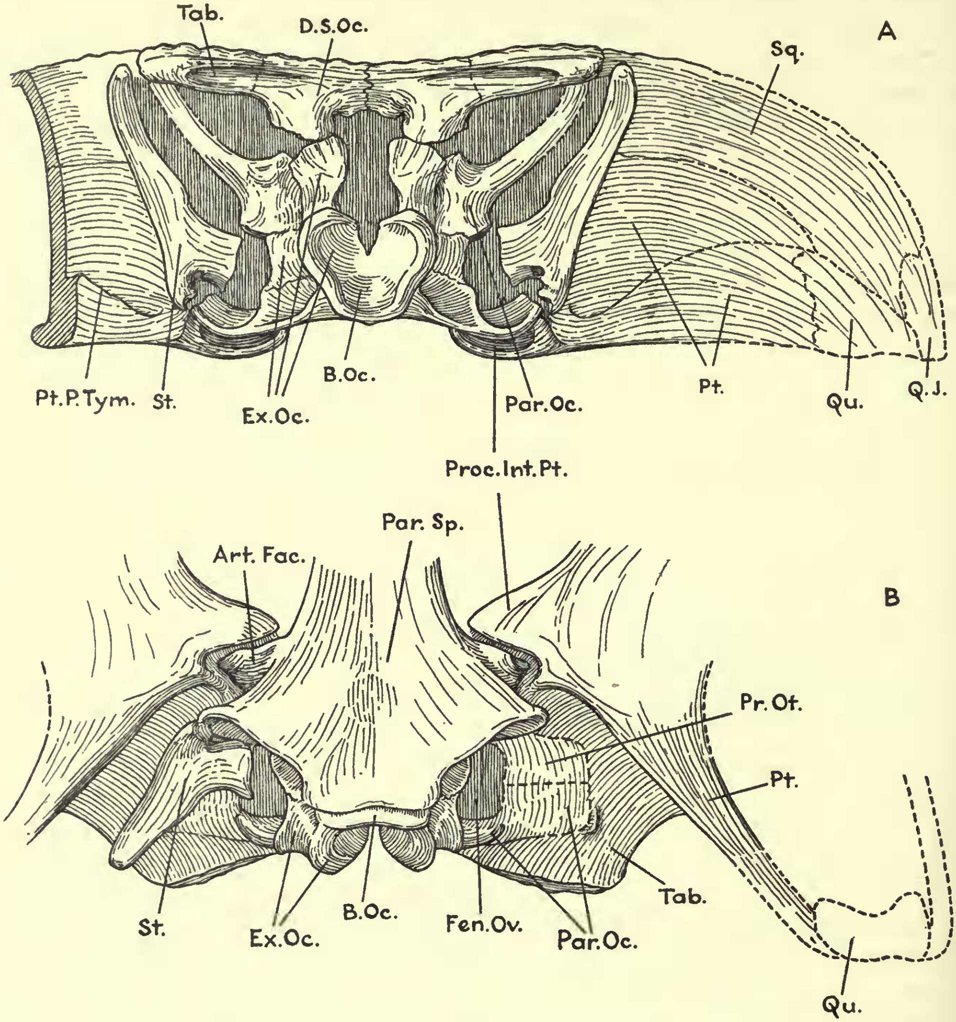
TEXT-FIG. 21.—*Trimerorhachis* sp. (B.M.N.H., R.576). × 1½. Posterior part of the parasphenoid with hinder part of the brain-case articulated with it (compare with Text-fig. 20). A, From above; B, from the right side; C, from below. Reference letters as before with: *B.Oc.*, basioccipital; *Ex.Oc.*, exoccipital; *Fen.Ov.*, fenestra ovalis; *Par.Oc.*, paroccipital; *Pr.Ot.*, proötic.

widened mass clearly originally continued by cartilage, which is applied to—but extends laterally of—the front end of the base of the exoccipital. A groove on its hinder surface passing forward and inward completes the vagal foramen, and the upper end of the bone must touch the exoccipital and nearly reaches the skull roof. The bone is continued laterally by a massive paroccipital process, which is thin dorso-ventrally but wide from back to front. The outer end of this process is unossified, but clearly extended laterally as cartilage to be received in a depression on the lower surface of the tabular bounded laterally and posteriorly by an upstanding ridge. This depression lies far in front of the corner of the tabular at the inner side of the otic notch. Throughout the paroccipital is widely separated from the skull roof by a large post-temporal fossa. The lower surface of the paroccipital process is only shown in R.576, where it extends forward to meet the corresponding surface of the proötic, and admesially ends abruptly in a border lying parallel with the middle line, which is the upper margin of the bony fenestra ovalis.

The proötic is ossified in R.576. It is a bone much resembling the paroccipital, to which it is closely applied, the two together forming a wide but shallow process, with a wide groove running antero-posteriorly above it, which flares out on to the shallow anterior face of the proötic. Ventrally the proötic has a base descending into a mass of cartilage resting on the parasphenoid, and it forms the anterior part of the fenestra ovalis.

The stapes lies nearly in position on each side of one specimen (M.C.Z. 1169), from which Text-fig. 22 is drawn. In it the stapes is placed in position and is necessarily foreshortened. The bone has an almost straight outer border, which turns in at its lower end to the accessory process. The shaft of the bone is gently concave across its lower (posterior) surface, rounding over on the outer side, the inner forming a distinct edge. The inner border bows out from the bone a little in the middle of its length, but cannot have come into contact with the otic capsule. Distally the bone ends in a small rounded surface, whilst proximally the powerful accessory process turns a little inward and ends in a surface, at about 45 degrees to the length of the bone, which is itself thrown out into minor processes for an attaching ligament. This process is separated by a groove, into which opens the foramen for the stapedial artery, and a notch from the more powerful process which carries the footplate. This process passes inward at an angle of about 130 degrees to the shaft, is massive, and truncated by a slightly concave surface for attachment to the membrane closing the fenestra. It seems evident that this ancillary process was connected to the outer end of the lateral ridge of the parasphenoid, and that the distal end of the bone lay in the tympanic membrane, the footplate being thus brought squarely into the obvious position of the fenestra ovalis.

The pterygoid has a remarkable mode of articulation with the basis cranii. It is evident that the important attachment was between a face directed backward, and placed vertically on the posterior surface of a special inwardly directed process of the pterygoid, and the front face of the parasphenoidal process. Each of these two opposed facets is concave, so that it is evident that the joint—though firmly fixed—was flexible owing to the presence of a ligamentous pad between the two bones. The outer end of the posterior border of the articular process of the pterygoid swings round so as to limit a pit whose hinder wall is the beginning of an ascending rounded ridge passing upward and backward at the root of the quadrate ramus. Little space is left for a contact between the cartilaginous basipterygoid process and the



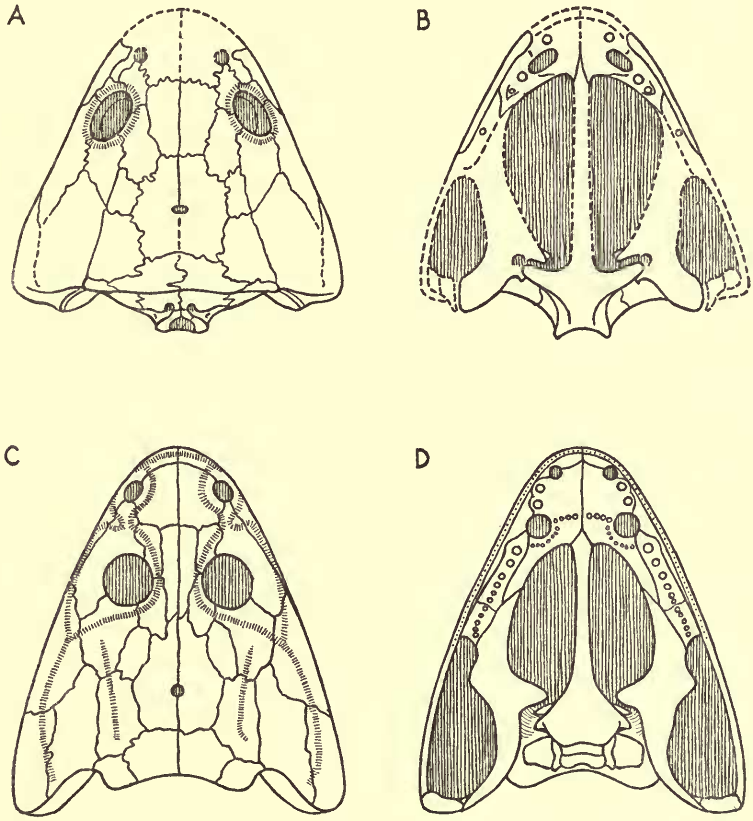
TEXT-FIG. 22.—*Trimerorhachis* sp. Reconstruction of the posterior part of a skull made from specimen M.C.Z. 1169. About natural size. A, From behind; B, from below (to be compared with Text-figs. 20 and 21). Reference letters as before with: *D.S.Oc.*, dermosupraoccipital; *Proc.Int.Pt.*, processus internus of pterygoid; *Pt.*, pterygoid; *Pt.P.Tym.*, post-tympanic ridge of the pterygoid; *Qu.*, quadrate; *Q.J.*, quadratojugal; *Sq.*, squamosal; *St.*, stapes; *Tab.*, tabular.

pterygoid. Apart from the special articular process (not otherwise known in described Texas Labyrinthodonts) the pterygoid generally resembles that of *Eryops*, though it possesses the groove bounded by a ridge on the posterior surface of the quadrate ramus, originally recognized by Sushkin as the floor of the tympanic cavity in *Capitosaurus*. The remainder of the structure of *Trimerorhachis* is well described by Cope, Broom, Williston and Case.

COMPARISON OF EOBRACHYOPS WITH TRIMERORHACHIS

Resemblances

Eobrachyops and *Trimerorhachis* are not very different in size; the type skull of *T. conangulus* Cope is about two-thirds as long as *E. townendae*, whilst most specimens



Text-fig. 23.—Skulls of *Eobrachyops* and *Trimerorhachis* reduced to the same width enabling them to be compared. A and B, *Eobrachyops townendae*, dorsal and palatal views; C and D, *Trimerorhachis* sp., from Cope's figures of the type skull of the genus, Broom's figures, and Case's 1935 materials.

of *T. insignis* are twice the size. The two animals resemble one another in the general outline of the skull, in the forward position of the orbits, and in their flat dorsal surfaces. The otic notches are small in *Trimerorhachis*, and absent in *Eobrachyops*. An intertemporal bone is present in each. The occipital condyle of each is a nearly circular concave face, largely made by the basioccipital. In each the pterygoid articulates "movably" with the parasphenoid by transverse faces. In each a pocket—apparently for the insertion of the recti capitis muscle—lies on the lateral surface of the parasphenoid not very far behind the articulation with the pterygoid. In each form the mandible is remarkable at this period in possessing a well-developed retroarticular process.

The vertebral columns are similar in the lack of fusion of the two halves of the neural arches in the anterior region, in the delicacy of the circum-notochordal elements, and in the large size of the notochordal sheath. The dermal shoulder girdles are similar in the presence of rhomboidal interclavicles, and in the wide expansion of the ventral parts of the clavicles, a condition otherwise unknown in the Texan Permian Labyrinthodonts—except in *Archeria* (= "*Cricotus*"). The two forms possess identical bony? scales. There is therefore a number of real resemblances between the two forms, and a further analysis is necessary.

Differences

The resemblance in general skull outline is purely superficial. The small otic notch of *Trimerorhachis* housed a tympanic membrane in which the stapes ended, *Eobrachyops* must have entirely lacked such a structure, no doubt a secondary condition associated with some change in the mechanism of hearing.

In *Eobrachyops* the quadrate lies far forward on the level of the occipital condyle, in *Trimerorhachis* it is relatively far back, at least in some specimens. In *Eobrachyops* the quadrate articulation is carried down by the deep cheek and lies far below the floor of the basioccipital, whilst in *Trimerorhachis* the quadrate condyle seems to be on the same level as the bottom of the occipital condyle.

In *Eobrachyops* the orbits are widely separate from one another and extend so far laterally that the depth of the jugal and maxilla below them is extremely small. In *Trimerorhachis* conditions are quite different, the face below the orbit being very deep. In the detail of pattern of dermal bones in the circumorbital region the two animals differ very greatly. In *Trimerorhachis* the lachrymal is a huge bone, extending from the nostril backward below the orbit to meet not only the jugal, but the postorbital. In *Eobrachyops* it forms scarcely more than one half of the outer border of the orbit, and does not reach the nostril.

Thus the occurrence of an intertemporal in each form is merely the retention of a primitive character, and there is no reason to suppose that the few resemblances between the skull roofs have any phylogenetic significance ; they have been derived, no doubt, from a common ancestral pattern by entirely different courses of change.

The basicranial and otic regions differ in the larger contribution which the exoccipitals make to the condyle in *Trimerorhachis*, and in the fact that in that animal there is no extension of the exoccipital over the paroccipital, whilst in *Eobrachyops* there is to such an extent that the vagal foramen lies entirely in the exoccipital. In *Eobrachyops* the paroccipital remains entirely cartilaginous, in *Trimerorhachis* it is well ossified.

In *Trimerorhachis* there is a special process from the parasphenoid which bears the articular face for the pterygoid, but in *Eobrachyops* this face is carried directly on the front of the great lateral wing of the parasphenoid.

The palate of *Eobrachyops* has larger interpterygoid vacuities than that of *Trimerorhachis*, as shown by the fact that the pterygoid does not meet the vomer. The two differ in the details of the dentition, and *Eobrachyops* is unique in that the vomer and palatine meet laterally to the internal nostril.

The lower jaw of *Eobrachyops* differs markedly from that of *Trimerorhachis* in its straight ventral border. The circumchordal elements of the vertebral column of *Eobrachyops* differ from those of *Trimerorhachis* in the much more parallel sides of the intercentra, which do not possess the typical rhachitomous wedge-shaped form of the latter genus. In the shoulder girdle the clavicles meet in front of the interclavicle in *Eobrachyops*, and not in *Trimerorhachis*.

Two Striking Common Features

Thus it appears that the two genera are not very closely related : their resemblances are dependent on the retention of primitive qualities and a somewhat similar skull shape. However, the special process of the pterygoid which articulates with the parasphenoid is common to both, and is a very unusual feature ; and the retention of a deep basioccipital as the greater part of the nearly circular condyle, whilst the basisphenoid is so greatly dorso-ventrally depressed that the movable attachment of the pterygoid to the basis cranii is essentially by means of a special facet of the parasphenoid, is a remarkable point of resemblance between the two genera, as it seems to be found in few other animals.

Characteristics of Eobrachyops are the Special Qualities of Brachyopids

The most striking special characteristics of *Eobrachyops* are (*a*) that the occipital condyle lies considerably behind the posterior margin of the skull roof ; (*b*) that the border of the pterygoid at the subtemporal fossa is suddenly carried upward so that the palate in this region is a broad ∩-shaped arch ; (*c*) that the quadrate condyle lies far below the ventral surface of the parasphenoid ; (*d*) that a distinct space, formerly occupied by a cartilaginous ridge on the posterior surface of the quadrate, separates the hinder border of the pterygoid from those of the squamosal and quadratojugal ; (*e*) that the outer surface of the squamosal and quadratojugal passes round on to the posterior face of the quadrate and there forms a laterally concave, nearly vertical surface.

These five characters are essentially those which I listed in 1919 (pp. 47–48) as special qualities of the Brachyopidae. Their occurrence in *Eobrachyops* and in no other Labyrinthodont except the Brachyopids and *Dvinosaurus* seems to me strong evidence for believing that *Eobrachyops* was the " prototype " of this group, in the sense that it was a Lower Permian representative rather than literally ancestral to any one of the later members.

Conclusion on Relationship of Eobrachyops to Trimerorhachis and Brachyopids

It is evident that *Eobrachyops* more greatly resembles *Dvinosaurus* and the Brachyopids than does *Trimerorhachis*. The latter lacks any sign of the deepened cheek which exists in all Brachyopids, and to a less extent in *Dvinosaurus*. It has often a considerable production of the quadrate condyle behind the occipital condyle, in contrast to the condition in Brachyopids. In *Trimerorhachis* the occiput is invisible from above (or nearly so) in contrast to the sloping occiput and very posteriorly placed condyles of Brachyopids, *Dvinosaurus* and *Eobrachyops*. In *Trimerorhachis* the pterygoid at the inner border of the subtemporal fossa is bowed inward mesially to the inner surface of the jaw, and is not at all produced downward. In *Dvinosaurus* this border is . . . " strongly inclined ventralwards by its end correspondingly to the general vaulting of the palatal surface " (Sushkin, 1936 : 56), but it does leave a small part of the subtemporal fossa visible within the lower jaw. The pterygoid of the Brachyopids differs from that of *Trimerorhachis* in ways which carry the differences shown by *Dvinosaurus* to their logical conclusion, but *Eobrachyops* has the Brachyopid condition in an extreme form.

In *Trimerorhachis* there is a functional otic notch, and a stapes of normal Labyrinthodont type ending in it. In *Dvinosaurus* and *Batrachosuchus* the stapes is greatly deepened distally, its end being tied down by ligament to that posterior surface of the ridge of the quadrate which separates the occipital part of the squamosal from the pterygoid. It is indeed not easy to imagine intermediate stages between the two conditions, whilst the resemblance between the stapes of *Dvinosaurus* and that of *Batrachosuchus* is obvious (cf. Sushkin, 1936 : 59).

In *Trimerorhachis* the lachrymal is immensely enlarged and separates the orbit widely from the maxillary border, in *Dvinosaurus* (Bystrow, 1938) it is less extensive and the space between the orbit and the maxillary border smaller. In Brachyopids it is still further reduced.

The comparison can be extended to many other features with the same conclusion : that *Trimerorhachis* may well have some real relation to *Eobrachyops*, but that the latter in all ways makes a better ancestor for *Dvinosaurus* and the Brachyopids.

EOBRACHYOPS COMPARED WITH PELION

Sushkin, when he recognized the remarkable processus internus of the pterygoid of *Dvinosaurus* and showed its resemblance to that of *Trimerorhachis*, could only add as a parallel *Archegosaurus* as I figured it (1919, fig. 2). But it also occurs in the Coal Measure *Saurerpeton* and *Erpetosaurus* described by Romer (1930, 1947) and Steen (1931). I therefore examined Steen's materials of these animals in the British Museum. Dr. Steen had prepared them by removing the surviving remnants of bone by hydrochloric acid, thus getting exquisitely perfect impressions from which she could make squeezes in plasticene or dental wax only. But, as Mr. Donald Baird of Harvard showed me, it is possible to make casts from such moulds with rubber latex loaded with an opaque powder. Casts so made are incomparably better than any at Dr. Steen's disposal, and enable me to add some details to her perfectly accurate accounts of these animals.

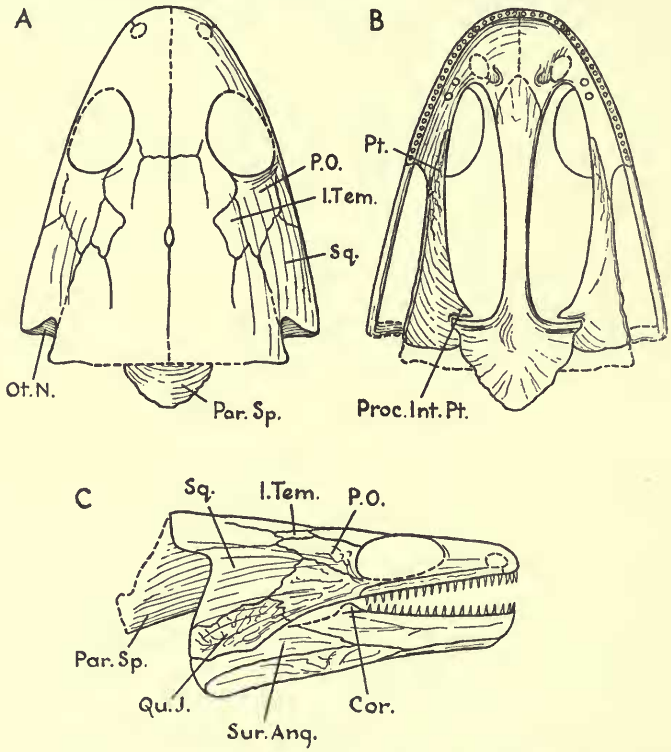
Identification of Pelion lyelli

Specimen B.M.N.H., R.2674, was described as *Pelion lyelli*, though Dr. Steen (1931: 874) notes that it differs materially from Romer's description of two skulls referred to that species in 1930. In 1947 Romer (without resolving the differences which Steen mentions) refers the three specimens in question to Moodie's genus *Saurerpeton*, founded on one of the specimens. *Pelion lyelli* has as type a partial skeleton so covered by a film of matrix that no real knowledge of its skull structure can be gained.

To *Pelion* Romer (1947) now refers a skull (described by Moodie as *Erpetosaurus tabulatus*) for which he founded a genus *Branchiosauravus* in 1930. Romer (1930, fig. 7) draws (but leaves unshaded) a bone projecting behind the table. This bone in Moodie's photograph (1916, pl. 25, 2) seems to lie below the skull roof and to have a pair, less evident, but a good match. It is possible that these are the remains of an occiput, stretching backward behind the occipital border of the table as that structure must have done in Steen's *Pelion*. Thus it is probable that the two animals belong to the same species, Moodie's being older than Steen's, as it is half as large again.

Re-examination of Pelion

Steen's specimen of *Pelion lyelli* may be described from the cast as follows. The skull lies on its dorsal surface, both lower jaws being in position, articulated with the quadrate condyles. On the spectator's right (animal's left) side the cheek is completely flattened out into the plane of the table, the lower jaw is seen—dorso-ventrally compressed—directly from below, but with the border of the pterygoid at the sub-temporal fossa squeezed down into contact with its inner surface. This crushing has disarticulated the pterygoid from the basis cranii, which, although crushed down on to the skull roof, is still nearly symmetrically placed with respect to the eyes. The right lower jaw is in articulation with the quadrate, but has become detached at the symphysis and straightened, by pressure, lies so as to show the whole of its outer surface. Its lower border has squeezed and broken the lower part of the pterygoid where it forms the border of the sub-temporal fossa. The right maxilla, jugal and quadratojugal lie in nearly natural articulation with each other and with the quadrate and lower jaw, and are inturned so that their outer surface is shown. Steen, in her accurate drawing (text-fig. 15), shows the large parasphenoid with a rather definitely marked short blunt-ended basipterygoid process. The new cast shows that this structure has its anterior edge drawn downward, so that there is a large somewhat concave face directed forward to which a corresponding facet of the pterygoid was attached. On the spectator's left the corresponding process is shown with a special " processus internus " of the pterygoid in articulation with its flat front face. On the spectator's right Steen's fig. 15 shows quite accurately a strange hook-shaped mesial edge to the pterygoid, which in her restoration she attached to the outer end of the parasphenoid process, but in the same figure she shows with a dotted line a break in the inner border of the palatal process of the pterygoid. It is evident from the new cast that this is the real processus internus, with a flat surface directed backward for articulation with the anterior deepened face of the parasphenoid, the whole agreeing exactly with the structure seen on the animal's right. The pterygoid extends outward from this articulation as a relatively enormous sheet of bone somewhat cracked and crumpled but evidently continuous to a border, which is pressed against the inner surface of the lower jaw for a very long distance, to



Text-fig. 24.—*Pelion lyelli* Wyman. Reconstruction of a skull (B.M.N.H., R.2674). × 2·2. a, Dorsal; b, palatal; c, right lateral aspect. Reference letters as before.

the middle of the orbit in fact. The lateral strip of this bone bears an ornament of ridges and grooves, deeply cut and of most unusual character. The sculptured strip extends very far forward, but ends posteriorly a little in front of the level of the basitemporal articulation. Steen held that this strip was made by palatine and transverse bones, but the right lower jaw shows a coronoid process in position with respect to the jugal and maxilla, which determines the anterior end of the subtemporal fossa, and thus of the hinder end of the transverse bone; it lies much too far forward to make Dr. Steen's interpretation plausible. Furthermore, the ridges of the ornament on the presumed "ectopterygoid" continue the direction of those on the pterygoid, as they would be unlikely to do across a suture.

It is thus evident that Dr. Steen (and Dr. Romer) were unjustified in regarding this skull as broad and low, and it remains to determine its shape.

As Steen recognized, the left premaxilla is in position and the series of teeth it supports clearly shown. The parasphenoid—a little laterally bent—is in articulation with the anterior part of the palate, and the dorsal surface of the skull—though the sutures connecting its bones opened a little when it was spread out flat—is essentially intact. It is evident that the part of the pterygoid which on the spectator's right lies mesial of the basicranial articulation is the parotic plate, which in life was essentially vertical.

Thus reconstruction of the skull shape is a matter of fitting measurements so that dorsal, ventral and lateral views are self consistent and provide projected transverse sections which give proper measurements. I began with the right maxilla, jugal and quadratojugal, which show that the lower border of the cheek turns downward from the direction of the straight maxillary border. The otic notch of the left side and upper part of the squamosal in front of it are shown ; they allow the depth of the cheek at its hinder border to be measured, and the size and shape of the right quadratojugal and jugal fix the outline of the squamosal, though there is a possible foreshortening by obliquity in direct side view. The width of the table, between the otic notches, is shown for the left side, the interorbital width and the sizes and shapes of the postfrontal, postorbital, intertemporal and supratemporal are known, and in no Labyrinthodont is the table more than gently curved. Thus trial sections give possible proportions. The skull shape so determined, with its very characteristic down-turning of the lower border of the cheek behind the orbit, was then fitted to the lateral aspect of the lower jaw as shown directly on the animal's right, the jaw being shortened because it is a curved structure which has been laterally flattened into a straight one.

The resulting fit is surprisingly good. Finally the palate has to be fitted in. The distance measured from the most lateral point of the basitemporal facet of the pterygoid to its lateral border is known. The distance from the most dorsal point of the parotic plate to the border of the pterygoid is known. The lowest possible place for the outer border of the pterygoid with respect to the lower jaw is known. Thus trial transverse sections made by measurements of individual bones along correctly determined directions allow small modifications to be made until everything fits. Finally the parasphenoid has to be put into place. The reconstruction of the skull carried to the present point has fixed the position of the facet for articulation of the pterygoid with the parasphenoid. The parasphenoid is still in position with respect to the premaxilla. Direct measurements made on the skull photograph show that the distance from the front point of the interpremaxillary suture to the articular facet on the pterygoid agrees exactly with that for the pterygoid on the parasphenoid, when the measurement is made on a trial longitudinal section of the skull. Thus the slope of the bone in side view is established, the total length from the anterior end of the skull to the hindmost point of the parasphenoid is known, so that the position of the occiput is fixed with considerable certainty. The results are shown in Text-fig. 24. It may be added that there are no traces of any cartilage bones in the brain-case, so that the animal was probably very young.

Probable Relationships of Pelion

As so restored *Pelion* has notable resemblances to *Eobrachyops*. The two agree in having anteriorly placed orbits and a shallow face, behind which lies a long post-orbital skull with a wide table, cheeks sloping steeply downward, a lower border which passes downward from the hinder end of the short maxilla (at the level of the hindmost point of the orbit) to a low-placed quadrate, and an occiput which slopes backward below the hinder border of the table. The shape of the intertemporal is very much the same in the two animals, which implies that the mutual relations of all the bones in the postorbital region are very similar. In each the interpterygoid vacuity is very large, and the palate deeply vaulted as a result of a great widening of the pterygoid and the down-turning of its lateral strip mesial to the masticatory muscles. *Pelion* and *Eobrachyops* have an identical mode of articulation between the hinder surface of a processus internus of the pterygoid and a vertical facet on the laterally widened anterior border of the parasphenoid. In each animal the lower jaw has a very unusual straight lower border, and an upstanding coronoid process, not including any contribution from the surangular, conditions otherwise unknown in Labyrinthodontia except in *Dvinosaurus* and the Brachyopids. But *Pelion* retains an otic notch, a structure no doubt found in all primitive Labyrinthodonts, but lost in *Eobrachyops*, *Dvinosaurus* and all other Brachyopids. Thus it is not improbable that *Pelion* is closely related to the ancestry of *Eobrachyops*, and hence to that of *Dvinosaurus* and the Brachyopids.

EOBRACHYOPS COMPARED WITH ERPETOSAURUS

My attention was called to *Pelion* in this connection by the existence in it of the processus internus of the pterygoid, and, as *Erpetosaurus* has a similar structure, that animal should also be reconsidered.

Description of Erpetosaurus Material

Dr. Steen's material includes a skull (*E. radiatus*) in counterpart, so that an imperfect dorsal surface (R.2672) and a wonderfully preserved hinder part of the palate (R. 2670a) are available, together with an interclavicle, vertebrae and scutes (R.2672). A second skull (*E. laevis* B.M.N.H., R.2662) shows a well-preserved ventral surface, of which only the right hinder corner is missing, and another slab (R.2660) contains an interclavicle, scutes and vertebral elements. I have rubber casts of this material for comparison with Dr. Steen's descriptions, and can confirm them, adding something because my casts are so much better than her squeezes.

No. R.2670a retains the impression of the hinder part of the palate of a skull whose dorsal surface is shown by R.2672. This skull has the lower jaw of each side articulated with the quadrate, so that only small parts of this bone are visible. The pterygoids, though broken into parts by cracks, are perfectly preserved in detail and can be restored without difficulty. The ventral surface of the parasphenoid, and left side of the brain-case—much dorsoventrally flattened but otherwise well preserved—are visible, but a short misplaced rib running antero-posteriorly below a lappet belonging to the parasphenoid introduces some difficulties. The basioccipital is perfectly preserved, uncrushed, in articulation with the parasphenoid. The right exoccipital has swung round so that the whole of its posterior surface is shown, whilst the left retains its natural position, but is dorso-ventrally compressed. The parasphenoid is very well shown, and the left stapes is in its natural place.

Thus from enlarged photographs, on which the outlines of all important structures are inked in, it is possible by trial and error to restore the whole occipital region, measurements made directly from the casts with proportional compasses set at the magnification of the photographs giving constant control and guidance. The results are set out in Text-figs. 25 and 26, which in most matters explain themselves, but are here supplemented by notes on some points.

Brain-case

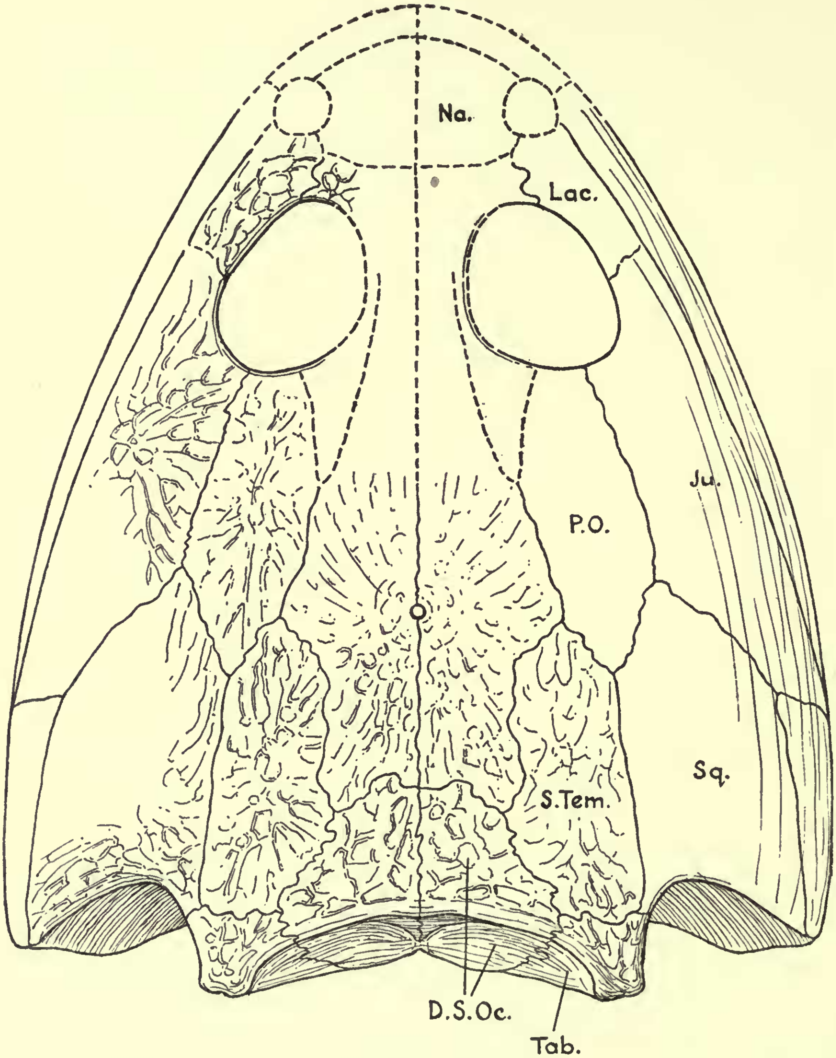
Occipital condyle. The large basioccipital has a widened, trumpet-shaped hinder end in front of which the bone narrows until it is surrounded by a ridge on the hinder part of the parasphenoid, which overlaps it at a very obvious denticulated suture. The " condylar surface " is a very deep conical pit. Each exoccipital bears a large concave articular surface lying largely lateral to the foramen magnum, joining the surface by which the exoccipital is attached to the basioccipital.

Occipital surface. The exoccipital is a very large thin sheet of bone of elaborate shape. It is evidently mainly perichondral bone sheathing the paroccipital so completely that it stretches far out beyond the vagal foramen, and wraps round the lower surface of the otic capsule, mesial of the fenestra ovalis, so that its anterior border has a long contact with the hinder border of the parasphenoid.

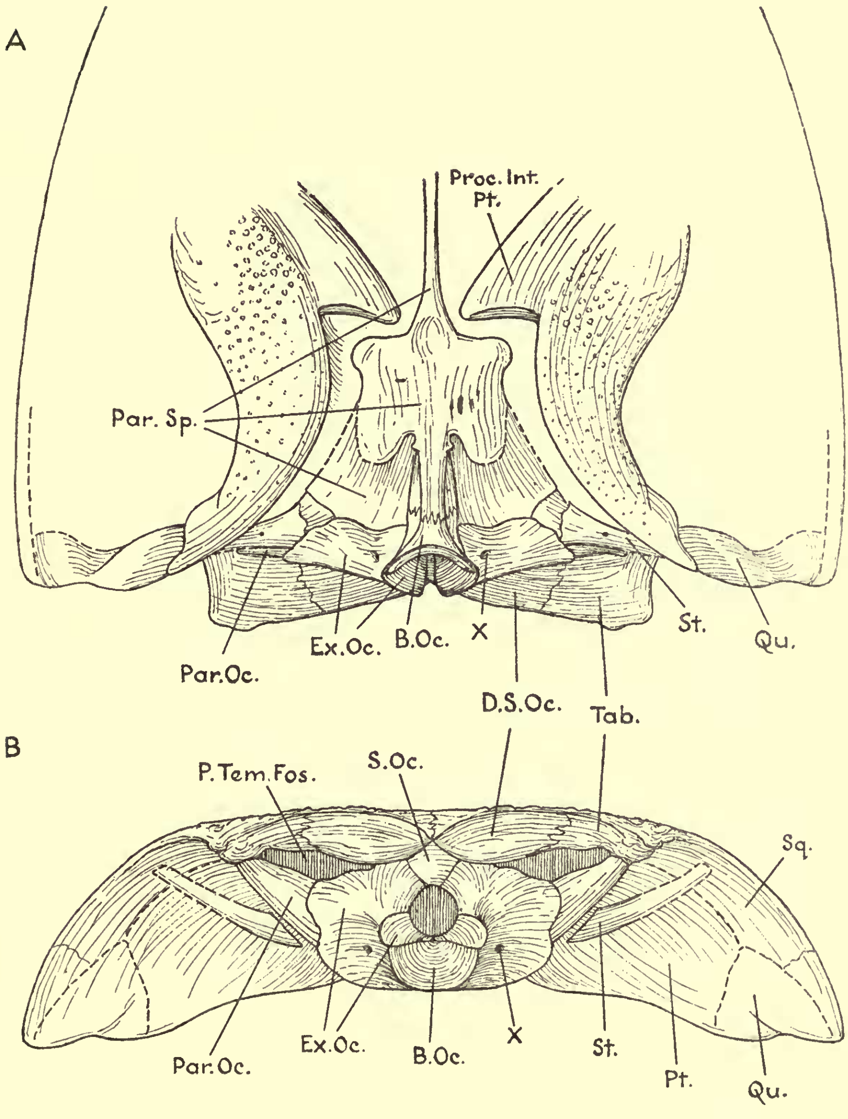
Supraoccipital. About one-half of the posterior surface of a supraoccipital showing part of the border of the foramen magnum is seen in articulation with the right exoccipital.

The *parasphenoid* is seen from below, a little hidden by a rib which is overlapped by a free ventral lappet of parasphenoid, and partly concealed on the other (right) side by a displaced ventral scute and fragments of pterygoid. The bone is cracked transversely, the hinder part—when viewed from below—lying some half millimetre dorsal to its original continuation. This is interpreted in Dr. Steen's restoration (text-fig. 1) as a pocket, but is shown by the new cast to be no more than a crack. Behind this fracture the parasphenoid bears a wide median ridge whose ventral surface becomes rounded posteriorly where it sheathes the basioccipital. The sides of this ridge are almost vertical, but pass into the wide lateral expansions of the hinder part of the bone. These pass backward until they meet the anterior borders of the exoccipitals. Lateral to this contact the border passes outward and forward, overlapping the proötic nearly to the border of the fenestra ovalis.

The *paroccipital* is represented only by a completely crushed but bony outer end, lateral to the exoccipital. The left stapes is present in position. It is a powerful bone with a wide flat foot, narrowing rapidly until it plunges under the quadrate



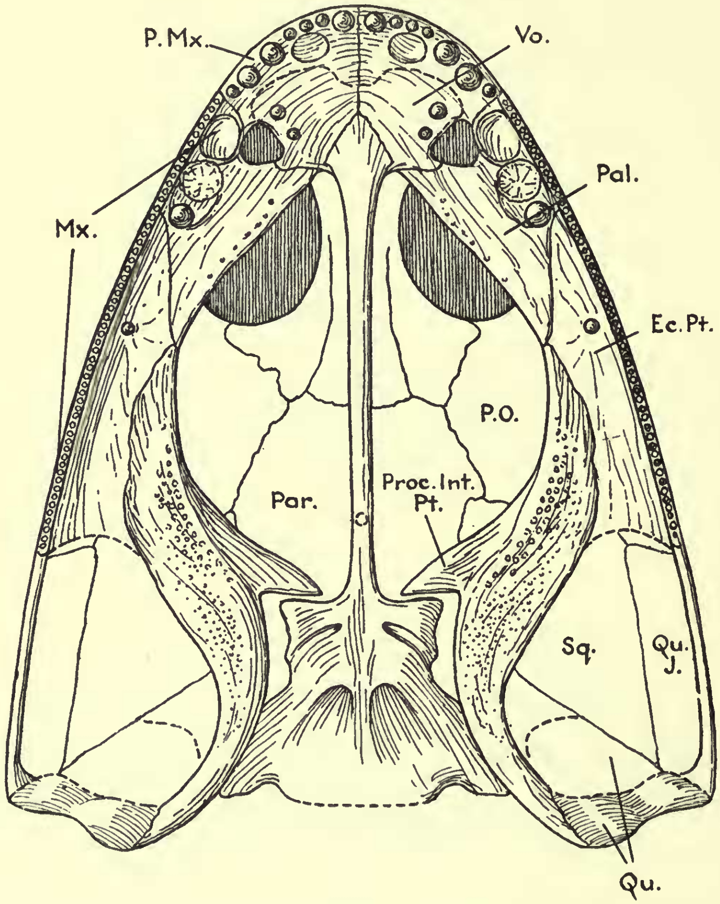
TEXT-FIG. 25.—*Erpetosaurus radiatus*. Reconstruction of a skull (B.M.N.H., R.2670a). × a little more than 2. Dorsal aspect. (Text-fig. 26 is of the same individual.) Reference letters as before.



TEXT-FIG. 26.—*Erpetosaurus radiatus* (B.M.N.H., R.2672 and R.2670a). × a little more than 2. Reconstructions A, of the hinder part of the palate, and B, occiput. Reference letters as before.

ramus of the pterygoid and is lost to sight. A very small perforation, presumably for a stapedial artery, enters its ventral surface far laterally.

Tabular and dermosupraoccipital. These bones lie largely on the dorsal surface of the table, but posteriorly they are deeply depressed where a pair of muscles spread forward from the neck to overlap small rounded areas. These areas are bounded anteriorly by a step rising to the highly ornamented dorsal surface of the skull, and are largely visible from behind.



TEXT-FIG. 27.—*Erpetosaurus laevis* (B.M.N.H., R.2662). ×2¼ approx. Reconstruction of the palate. The dotted circle in the processus cultriformis of the parasphenoid is the position of the pineal foramen. Reference letters as before.

PALATE

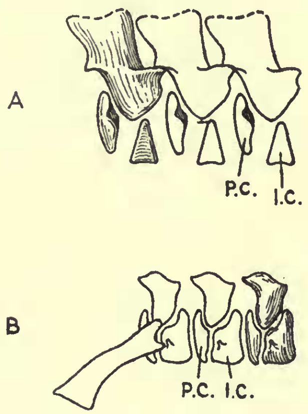
The palate as a whole is shown in *E. laevis* (R.2662), specifically distinguished by Dr. Steen from R.2670a described above. The distinction is valid, the parasphenoid of R.2662 lacking the free lappets of the other animal and bearing two grooves leading to foramina for the carotids, absent in R.2670a. They are, however, similar in all important known characters. R.2662, though well-preserved and nearly complete, is very difficult to interpret because the dentition is most unusual. The maxilla has slid downward and outward over the palatine, and the great premaxillary teeth have crushed forward and outward. Except anteriorly my figure agrees rather better with Dr. Romer's than with Dr. Steen's, whilst the difficult premaxilla is unlike either previous drawing.

Vertebral Elements

The specimen R.2672 of *Erpetosaurus* has associated with the skull an interclavicle and some other bones, together with some vertebral elements and very many scutes. Dr. Steen has described and figured most of these, but the new cast makes it possible to describe some vertebrae. A single intercentrum is seen end-on as a crescent-shaped bone, exactly like that of *Trimerorhachis*. It is a short segment of a cylinder of bone surrounding a notochord of large diameter and very little constricted. Its visible semicircular border is sharp-edged and a little out-turned. It bears no visible rib attachment. Closely associated are three pleurocentra. They are exposed from their outer surfaces and, except for a transverse fracture of one, show very little evidence of curvature to surround a notochord. They taper a little to each end, and have part of the upper end of one margin everted so as to leave an articular facet directed outward and either forward or backward. The two elements of a single unfused neural arch agree, except that the spine of one stands across the bedding and is crushed down and incompletely shown. The neural arch element has a high spine widening as it passes upward ; its hinder border comes down on to the postzygapophysis, whilst the anterior border is at the root of the anterior zygapophysis. There is no transverse process, or sign of rib articulation. Text-fig. 28, A, is a restoration from these elements.

Another slab from Linton (B.M.N.H., R.2660) shows very many ventral scutes, and part of the inner surface of an interclavicle, which resemble those of *Erpetosaurus*. It is not capable of definite determination, but in many ways agrees with the original (R.2664) of Steen (pl. 4, fig. 2) showing twenty-five or more of the " triangular plates " which she figured. In this specimen the following matters seem certain (*a*) that all the elements are paired, none fused into cresent-shaped intercentra, as is the single example in R.2672 ; (*b*) all these bones have an internal surface toward the notochord which appears granular, and a smooth outer surface ; (*c*) two types are present, intercentra and pleurocentra. An intercentrum widens toward its lower border, which turns in under the notochord but does not meet its fellow, and has a blunt dorsal end. The hinder border is cut into by a rounded depression for surviving cartilage continuous with the neural arch, the rib head being connected by a ligament to a small pimple in the middle of the side of the bone. The other element, a pleurocentrum, is somewhat deeper than the intercentrum, and narrows both above and below. It bears an articular facet cutting into the summit of the anterior border of its smooth outer surface. The neural arch is very poorly shown, though there is an example in articulation with an intercentrum and pleurocentrum (Text-fig. 28, B) ; in no case is there any sign of a transverse process. I can only assume that here and in *Erpetosaurus* the rib articulated with the neural arch and pleurocentrum where the facet existed, and that in the present specimen its other head was tied to the " pimple " without any contact. There is evidence that the rib forks, one of the " heads " having a pointed, non-articular tip. The differences from the *Erpetosaurus* vertebrae already described may well be due to differences along the length of the column.

Thus the structure of *Erpetosaurus* is relatively well known, and its systematic position should be easily determinable. The vertebral column, as Dr. Steen has shown, agrees with that of the contemporary *Stegops*, and is of a type found in the Middle Rothliegende *Acanthostoma*, where as she states (1937 : 499), " both pleura- and intercentra being ossified as right and left hemicylinders, unfused in the mid-dorsal or mid-ventral line." Romer (1947 : 169) doubts this interpretation, suggesting that the intercentra shown in Steen (1937, text-figs. 4 and 5) are twisted round



TEXT-FIG. 28.—A, *Erpetosaurus radiatus* (B.M.N.H., R.2672). Reconstruction from scattered elements of three vertebrae from the right side. The intercentra are single ; B, ?*Erpetosaurus* (B.M.N.H., R.2664). Three vertebrae and a rib from the right. The shaded set of elements is drawn as it actually occurs. The intercentra are paired. All about 2 diameters.

and seen from below. I have examined casts of the specimen and its counterpart, which are not good enough to permit any definite conclusion, but Dr. Steen, with the original slabs before her, is unlikely to have been wrong in such a point.

Thus these vertebrae differ from ordinary rhachitomous vertebrae (*a*) in the absence of a transverse process well separated from the parachordal part of the neural arch, (*b*) in the usual existence of paired intercentra, which sheath the notochord for a large part of its circumference, (*c*) in the very high pleurocentra which extend over a very large part of the notochord. They are what Romer (1947 : 64, fig. 11) calls protorhachitomous, which by further ossification could well become embolomerous. *Stegops* is supposed by Romer to be related to *Acanthostoma*, which is evidently close to *Zatrachys*. If these views be justified then we have for the first time direct evidence of the evolution of typical or nearly typical rhachitomous vertebrae from such a protorhachitomous type.

Similarities Between the Two Forms

Thus, except for the processus internus of the pterygoid and its mode of articulation with the parasphenoid, there is in *Erpetosaurus* no resemblance to *Eobrachyops* such as that which *Pelion* shows ; but the vertebrae of *Eobrachyops* are " protorhachitomous", comparable with those of *Erpetosaurus* and *Stegops*.

PLATYSTEGOS LORICATUM Dawson

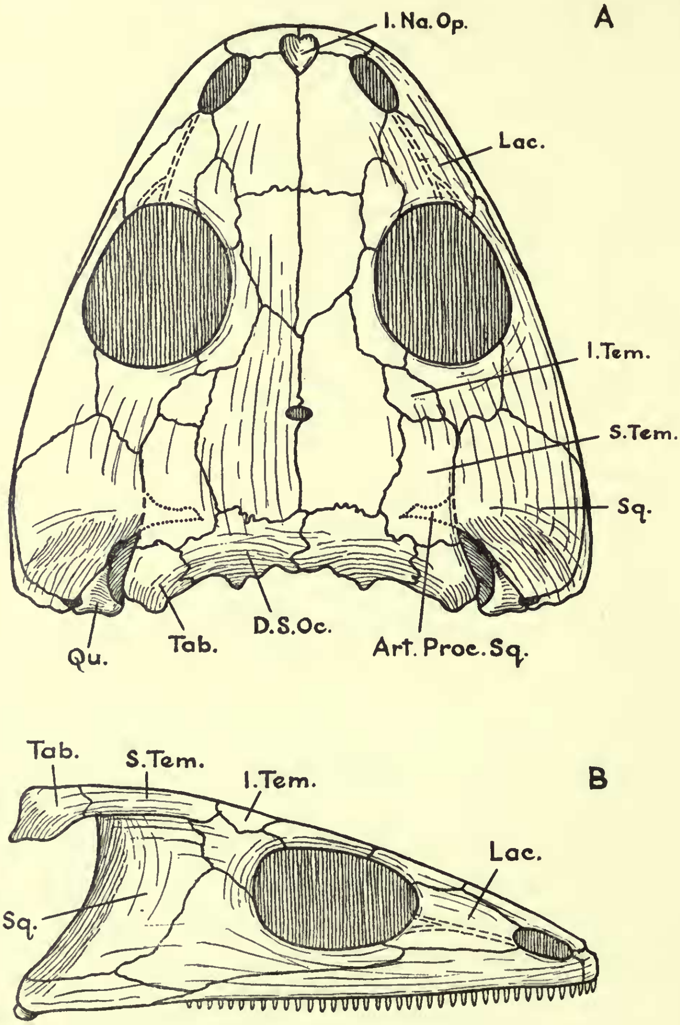
Description of Material

Another, earlier, Labyrinthodont, with a processus internus as a mode of articulation of the pterygoid with the parasphenoid, is an incomplete skull, apparently referable to *Platystegos loricatum* Dawson, from the Coal Measures of South Joggins, Nova Scotia, described by Dr. Steen (1934 : 480, 481). The South Joggins section is thick—11,000 ft. according to Dawson—and the amphibia come from the interior of hollow lepidodendroid trunks which stand on coal seams. Most are from Division IV, Section XV of the section ; this is about half-way up. The evidence of age comes mainly from plants, but according to Bell (1944) they are Westphalian B. Bell noted that the whole series does not extend high enough to reach the first occurrences of *Anthraconauta phillipsi*, but contains molluscs compared to *Anthracomya* cf. *modiolaris*. Thus the series seems to correspond to the Middle Coal Measures of Staffordshire, and the horizon of *Platystegos*, though above that of *Eugyrinus wildi*, is well below that of Linton and Nýřany.

This skull (D.M.S.W., B.95) shows the lower surface of a skull table with the upper part of the right orbit and the face in front of it. The block containing this complex of bones fits on to two others, one of which retains a mould of the lower surface of the table and the hinder parts of the two pterygoids, the left essentially in natural position though forced a little (perhaps 3 mm.) upward, the right misplaced. The third block continues the latter and shows the outer surface of the left side of the skull from premaxilla to quadrate, the quadratojugal being misplaced and lying in the orbit. The right pterygoid extends forward until it overlaps the vomer and palatal bones, whose upper surfaces are shown. The jugal of this side is detached and visible from nearly all aspects. The brain-case is completely missing, but one ramus of the lower jaw is largely seen.

Structure of Skull

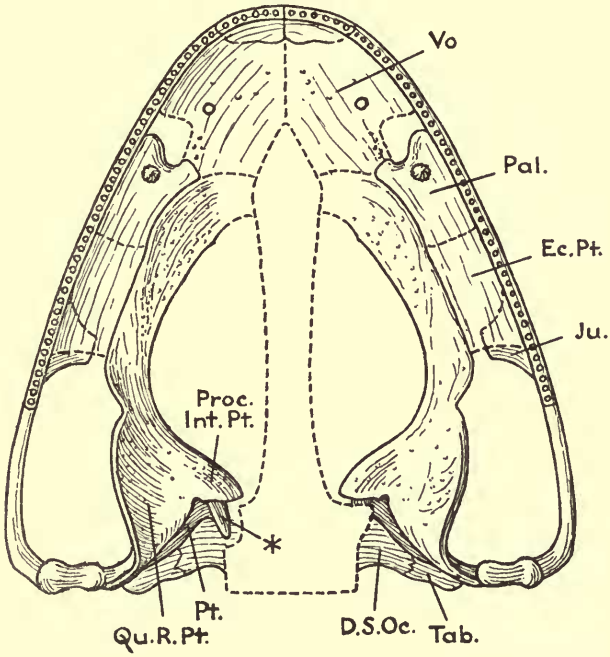
The general structure is clearly shown in the drawings in Text-figs. 29 and 30 which, though restorations, are carefully measured projections based on adequate, undistorted remains. The skull is short and broad, a little less than half its maximum breadth in height. The orbits are large and in the middle of the length, and the otic incision is overhung by the tabular, which forms a short process behind it. The hinder border of the dermosupraoccipitals and tabulars is turned downward, and there is some evidence that the occiput extended considerably behind the table and the quadrate condyles. There is a well-defined scar on the inner surface of that ridge of the tabular which forms the upper border of the tympanic notch which can only have articulated with the end of the paroccipital process. It is thus evident that no process passed inward from the tabular in contact with the upper surface of



Text-fig. 29.—Skull of *Platystegos loricatum* Dawson. (D.M.S.W., B.95) × 1½. Restored drawings of the skull. The sutures on the skull roof are taken from the lower surface. A, Dorsal aspect; B, right side. *Art.Proc.Sq.*, articular process of the squamosal for attachment to the supratemporal; *D.S.Oc.*, dermosupraoccipital; *I.Na.Op.*, internarial opening; *I.Tem.*, intertemporal; *Lac.*, lachrymal; *Qu.*, quadrate; *S.Tem.*, supratemporal; *Sq.*, squamosal; *Tab.*, tabular.

the paroccipital and below the post-temporal fossa. This condition exists in the Loxommids, but has been lost in all other Labyrinthodonts. There is an intertemporal bone separating the supratemporal from the postfrontal, and the lachrymal —which shows the course of the duct with its two canaliculi from the orbit—forms a large part of the orbital margin and the hinder border of the nostril.

The squamosal is remarkable because it is not attached suturally to the outer margin of the supratemporal. It abuts against it, the bone being 1·5 mm.—or a little more—in thickness in a skull some 5 cm. long. To strengthen this attachment

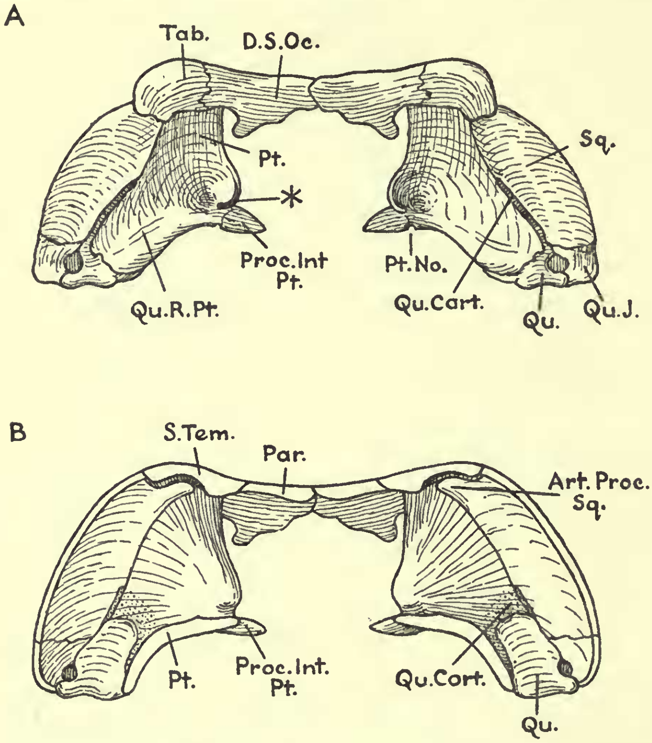


TEXT-FIG. 30.—Skull of *Platystegos* as in Text-fig. 29. × 1½. Palate. *D.S.Oc.*, dermosupraoccipital; *Ec.Pt.*, ectopterygoid; *Ju.*, jugal; *Pal.*, palatine; *Proc.Int.Pt.*, processus internus of the pterygoid; *Pt.*, pterygoid; *Qu.R.Pt.*, quadrate ramus of pterygoid; *Tab.*, tabular; *Vo.*, vomer; * pterygoid process described in text, p. 381.

a special process arises from the upper end of the admesial border of the subotic flange of the squamosal; this process passes directly inward with its essentially flat but dimpled upper surface opposed to a special sharply marked depression on the lower surface of the supratemporal. This arrangement, which is seen on both sides of the specimen, implies a powerful, ligamentous attachment.

The left quadrate is well shown from behind. Its lateral border is notched immediately above the shallow but wide outer condyle by the quadratojugal foramen, and a narrow parallel-sided strip of its posterior surface extends upward, visible between the inner border of the sub-tympanic flange of the squamosal and the hinder border of the parotic flange of the pterygoid. Some distance above the bony quadrate the inner edge of the squamosal steps inward to meet the pterygoid, presumably above a cartilaginous upward extension of the quadrate. There is a considerable pterygoid flange of the quadrate.

The pterygoid is a remarkable bone, not to be matched in any other Labyrinthodont known to me. The attachment to the basis cranii is by a processus internus, whose lower surface is rounded from back to front. This is abruptly truncated by a face which evidently articulated with a flat transverse facet on the parasphenoid. The anterior margin of the process begins at a point mesially and bows forward to its



TEXT-FIG. 31.—Skull of *Platystegos* as in Text-fig. 29. × 1½. A, Posterior view of the skull, lacking brain-case; B, the posterior part of the skull, without brain-case, cut across about at the middle of the supratemporal and viewed from in front. Cut surfaces are left white. *Art.Proc.Sq.*, process of the squamosal which is applied to the supratemporal; *D.S.Oc.*, dermosupraoccipital; *Par.*, parietal; *Proc.Int.Pt.*, processus internus of the pterygoid; *Pt.*, pterygoid; *Pt.No.*, "notch" in the pterygoid; *Qu.*, quadrate; *Qu.Cart.*, cartilaginous continuation of the quadrate; *Qu.J.*, quadratojugal; *S.Tem.*, supratemporal; *Sq.*, squamosal; *Tab.*, tabular; * pterygoid process described in text, p. 381.

root. It there swings forward to continue as the border of a rather large interpterygoid vacuity. This border can be seen on the right side until it passes below a misplaced lower jaw and cannot be followed. But it is evident that the pterygoid is still wide when it reaches the vomer, and that it may well have reached the parasphenoid. The lower surface of the processus internus continues laterally without break into that of the body of the pterygoid, which lies mesial of the vacuity for the masticatory muscles, and extends down within them to a curved ventral border.

The processus internus lies so far back in the skull that the quadrate ramus is not distinguishable from the body of the bone. The ramus sheathes the pterygoid process of the quadrate, rolling over its ventral border so as to form a rounded transition from the horizontal body to the concave upper part of the quadrate ramus. The quadrate ramus thus sheathes the ventral border and posterior surface of the quadrate, extending forward and inward beyond that bone to rise to the skull roof, behind the articular process of the squamosal. This transversely placed part of the pterygoid has a free admesial border, whose lower end (marked * in Text-figs. 30, 31) —lying above and a little behind the processus internus—projects backward to a point not meeting any other bone. The posterior surface of the pterygoid, between this point, the skull roof and the quadrate, is a hollow cone, incomplete because it lacks a triangular strip of its ventral part between the quadrate and point *. That flange of the pterygoid which sheathes the temporal muscle ends anteriorly by its lower border rising abruptly to pass into the lateral border of the palatal part of the bone. It comes, if not into direct contact with, at least into the very near neighbourhood of, that internal process of the jugal which, as in the majority of Labyrinthodonts, lies dorsal to the ectopterygoid, and often extends behind it to form the anterior border of the subtemporal fossa. The whole palatal surface of the pterygoid seems to have been covered by a sparse granulation of small teeth, little more than hemispherical projections.

No definite part of the ectopterygoid is visible, but the anterior end of the right palatine is well shown from above and from the outer side. The admesial part of the bone is a thin sheet with a feather edge. This passes laterally into an upturned ridge whose lateral face is deep, rounded from dorsal to ventral borders, and longitudinally grooved, evidently in continuous contact with the maxilla. This border ends by sloping down as the upper surface of a deep notch, the hinder border of the palatal nostril. Immediately below this process the bone carried a tusk, circular in section, with a sharply-grooved base. The large vomer is overlapped by the anterior end of the palatine, mesial and anterior to which it has a wavy thin posterior border, presumably articulating with the pterygoid. It is evident that some part of the bone has a granulation of small blunt teeth, widely spaced, and similar to those of the pterygoid. There is evidence of a vomerine tusk placed perhaps mesial of and near to the anterior end of the palatal nostril.

The left premaxilla is present in place, attached to the admesial end of the left maxilla. The anterior part of the internasal opening is shown. The suture with the nasal and the bone's contribution to the border of the nostril are uncertain. Some of the premaxillary and maxillary teeth are shown, and justify the figures. The general shape is certain, as the left side of the skull from front to back is visible, giving no evidence of distortion except for an inturning of the maxillary lower border, and the other drawings are fitted into the space so determined.

The inner surface of the hinder end of the right ramus of the lower jaw is shown from above, and an irregular transverse section of its anterior part is shown on a fractured surface. The face on the articular for the quadrate is fully ossified, divided by a low ridge into inner and outer regions for the quadrate condyle. It is clasped by the surangular laterally, and the prearticular—which sheathes its inner surface and continues behind it to meet the surangular—forms with that bone a ridge on the posterior surface, penetrated by a circular canal presumably for the chorda tympani. The rounded bottom of a groove on the prearticular helps to isolate the ridge, which is unfortunately damaged by a chisel cut, but may have been a first beginning of a retroarticular process. In front of the condyle the upper border of the prearticular descends very rapidly so as to leave the cavity of the jaw widely exposed from within. Anteriorly, below the orbit, the jaw becomes shallow, nearly as wide as it is high, with a marginal row of teeth bounding a flat upper surface. Thus it is possible that the Labyrinthodont jaws from South Joggins, recognized by Dr. Steen (1934 : 487) as those which first exhibit the later Labyrinthodont retroarticular process, belong to *Platystegos*.

Comparison with Dendrerpeton and Eugyrinus

Platystegos is found with *Dendrerpeton* and a series of very similar forms described by Dawson and Dr. Steen. The proportions, safely determined in each case, show that they may reasonably be generically distinguished. But the two animals are very similar ; the pattern of the external skull bones is essentially the same, the general nature of the palate with its large interpterygoid vacuities apparently bounded by the pterygoids and parasphenoids alone is not too dissimilar, and a processus internus of the pterygoid articulates with the parasphenoid in each. In each the tabular has a descending process from its under surface behind the tympanic space, and the general outline of the ventral borders of the descending flanges of the tabulars and dermosupraoccipitals is similar. In each form, if we may judge *Dendrerpeton* by Steen's photograph (pl. 1, fig. 2) the subotic flange of the squamosal passes smoothly over a rounded surface to the outer side of the skull, there being no well-defined crest as a border to which the tympanic membrane could have been attached. The pterygoid of *Dendrerpeton* is not known to have the extraordinary conical form of the quadrate ramus which occurs in *Platystegos*, but it extends up to the skull roof (Steen, text-fig. 2g) in the same way, and there is evidence in B.M.N.H., R.4553 and R.4554 that the special process of the squamosal which supplements the straight abutment of that bone on the table in *Platystegos* actually occurs in much the same form.

The lack of an interdigitated suture between the squamosal and the skull table in Dendrerpetonts, whilst all other dermal skull bones are firmly attached in that manner, seems to show that the contact itself is of recent introduction into their structure, the development of the special articular process of the squamosal showing that a firm connection is desirable. Similarly in Anthracosaurs the squamosal alone of dermal skull bones fails to have a sutural attachment to the table, and is held in place by the intervention of the palatoquadrate cartilage. The only explanation of the long delay in the establishment of this connection so implied is the survival in their Osteolepid ancestors to a relatively recent period of the notch between the membrane bones of the cheek and table which existed in them.

The group of Dendrerpetonts is additionally characterized by the occurrence of bony scales, oval or shield-shaped, with a delicate concentric striation, together with faint radial striae. In many ways *Platystegos* recalls *Eugyrinus* (Watson, 1940 : 215) which is somewhat older and much smaller. The general pattern of the dermal skull bones is common to the two, though *Eugyrinus* possesses lateral line grooves, apparently absent in all Dendrerpetonts. Both have large occipital flanges from the tabulars and dermosupraoccipitals, and the large parotic flange of the pterygoid reaches the skull roof behind a special articular process of the squamosal in the same way. The mode of articulation of the pterygoid with the basis cranii is different, *Eugyrinus* not possessing a typical " internal process ", and rather resembling *Eryops*. *Eugyrinus* has a " pterygoid flange " against the lower jaw absent in *Platystegos*. The dermal scales of *Eugyrinus* have a general resemblance to those of Dendrerpetonts. But in their possession of large interpterygoid vacuities the two groups agree, differing very greatly from the contemporary Loxommids.

Comparison with Brachyopids

Eobrachyops is, for its time, of very advanced and specialized structure. It retains an intertemporal bone and has thus a skull pattern of normal early Labyrinthodont type. But its face is extremely flattened, and its temporal region deepened immensely. The mechanical effect is to enable the animal to open its mouth to an extraordinary extent, by the action of a musculus depressor mandibuli attached to a retroarticular process much longer than in any contemporary. The long temporalis muscle would secure a powerful snapping bite. The wide and deep arch along the palate, between the pterygoid flanges which pass down mesially to the temporal muscle, would enable a large prey to be swallowed and could house a large tongue. The sloping occiput is associated with a very posteriorly-placed condyle, and perhaps with the possibility of raising the head nearly vertical to the vertebral column, and the considerable area of membrane bone on the occiput provides for the attachment of powerful neck muscles.

The stapes of Brachyopids, known in *Batrachosuchus* and *Dvinosaurus*, is presumably a modification of the normal Labyrinthodont type, subsequent to the suppression of the tympanic membrane which must have existed in their ancestors if they were to possess a stapes at all. This loss of an otic notch is associated with a movement back of the point of contact of the squamosal with the skull roof, and involves a corresponding backgrowth of the parotic part of the pterygoid. In association with this change in shape a horizontal flange, essentially a development of the base of the processus internus, comes to arise abruptly from the inner surface of the pterygoid ; separating the parotic plate from that which sheathes the masticatory muscles almost down to their attachment to the mandible.

The quadrate is unique. Its flat inner surface is completely covered by the pterygoid, but the bone itself is exposed as a narrow vertical rib between the pterygoid and the admesial border of the squamosal. Laterally to the quadrate rib the squamosal forms a vertical hollow cylindrical face before passing over a rounded surface to the cheek.

Inspection of the figures of *Platystegos* will show that in many ways it makes a starting point from which the Brachyopids could have arisen. A deep ridge of quadrate is visible from behind between the pterygoid and squamosal, which turns a very little backward towards it. The posterior face is widely and shallowly grooved from top to bottom and it passes over a rounded surface to the outer side, there being no sharply defined ridge for the attachment of a tympanic membrane. The conditions differ from those in Brachyopids in the retention of a definite pterygoid ramus of the quadrate and of the pterygoid sheathing it. But these are common early Labyrinthodont features, which must certainly have existed in some ancestral Brachyopid.

The palate of *Platystegos* has, in the deep flange of the pterygoid which sheathes the masticatory muscles, a structure which alone could have provided the starting point of the Brachyopid condition. The mode of articulation of the pterygoid with the parasphenoid is the same in *Platystegos* and *Eobrachyops,* and the large interpterygoid vacuities provide conditions from which the relatively enormous vacuity of *Eobrachyops* could have arisen long before it is parallelled in most other Labyrinthodonts. It is, of course, most improbable that *Platystegos* is a real ancestor of the Brachyopids: all that can be claimed for it is that in some ways it possesses structural qualities which explain how those which characterize that group may have arisen. On the other hand *Platystegos* differs as completely as any Labyrinthodont can from *Erpetosaurus,* which seems to have been a rapidly advanced form with no known descendants.

Platystegos is also important because with its associated Dendrerpetonts and *Eugyrinus* it is the earliest known normal Labyrinthodont, other than the Loxommids, which retains obviously more primitive features in many structures in the skull, together with certain special peculiarities, and an advance in the mode of attachment of the squamosal to the table.

SURVEY OF BRACHYOPID LINE

We have thus by consideration of the structure of skulls (and lower jaws when they are known) reached the conclusion that *Eobrachyops townendae,* Clear Fork; *Eobrachyops casei,* Clear Fork; *Bothriceps australis,* ? M. Permian; *Dvinosaurus,* U. Permian; *Trucheosaurus,* U. Permian; *Brachyops,* Permo-Triassic boundary; *Batrachosuchus browni,* L. Trias; *Batrachosuchus watsoni,* L. Trias; "*Platyceps*" *wilkinsoni,* L. Trias; *Plagiosternum granulosum,* M. Trias; *Plagiosuchus,* M. Trias; *Gerrothorax,* U. Trias and Rhaetic; and *Plagiosaurus depressus,* ? Rhaetic; are members of a group of Labyrinthodonts relatively closely allied to one another, though not members of a single lineage. These come from Texas, Australia, Russia, India, South Africa, Germany and Sweden, and members of the group are known also from Argentina, Siberia and Spitsbergen. But ten species are known by a single specimen only, two from about three specimens each, and only *Dvinosaurus* is represented by a satisfactory suite of some seventeen. Such a mode of occurrence suggests that the evolutionary history of the group was complex, and the occasional recognizable existence of neoteny emphasises the probability. Furthermore, nothing in the known structure of a single young skull referred to *Pelion* from the Coal Measures of Ohio prevents its acceptance as an early member of the group, but it differs in some ways which will require discussion.

Thus it is evidently impossible to hope to find a true evolutionary series amongst these animals ; the whole group would probably have included a large number of species representing not only members of main stocks, but many blind-ended side-branches like *Dvinosaurus*, retaining, when sexually mature, larval qualities which may be (or may, like a frog's tadpole, not be) proper to a time earlier than that in which they lived.

Thus all we can do is to study the group as a whole, placing its members in order of time and recognizing such changes in structure as persist over all or some part of the long life of the stock. I did this (so far as the material allowed) in 1919 (p. 56) showing that the direction of change in structure was the same as in the Capitosaur-shaped skulls from *Eryops* to *Cyclotosaurus*.

The greatly extended knowledge contained in the present paper confirms that conclusion and extends it :

(1) The large mainly basioccipital condyle of *Eobrachyops* passes to the wide, tripartite condyle of *Dvinosaurus*, and that passes to the separated exoccipital condyles and absence of a basioccipital in *Batrachosuchus*, etc.

(2) The ossified supraoccipital of *Eobrachyops* and *Dvinosaurus* vanishes in the later forms.

(3) The widespread exoccipital of *Eobrachyops*, although reaching the tabular, does not extend forward to the pterygoid as it does to an increasing extent in *Bothriceps*, *Batrachosuchus* and the " Plagiosaurs ". The otic capsule contains no visible ossification in any form.

(4) The pterygoid, movably articulated with the parasphenoid in *Eobrachyops* and *Dvinosaurus*, gains a sutural attachment to the lateral border of the parasphenoid in *Bothriceps*, which steadily increases in extent by spreading backward to the exoccipital.

(5) Hypoglossal foramina perforate the exoccipital of *Eobrachyops*, lie on the lateral surface of that bone in *Bothriceps*, emerge through the hinder surface in *Batrachosuchus*, and have disappeared in *Gerrothorax*.

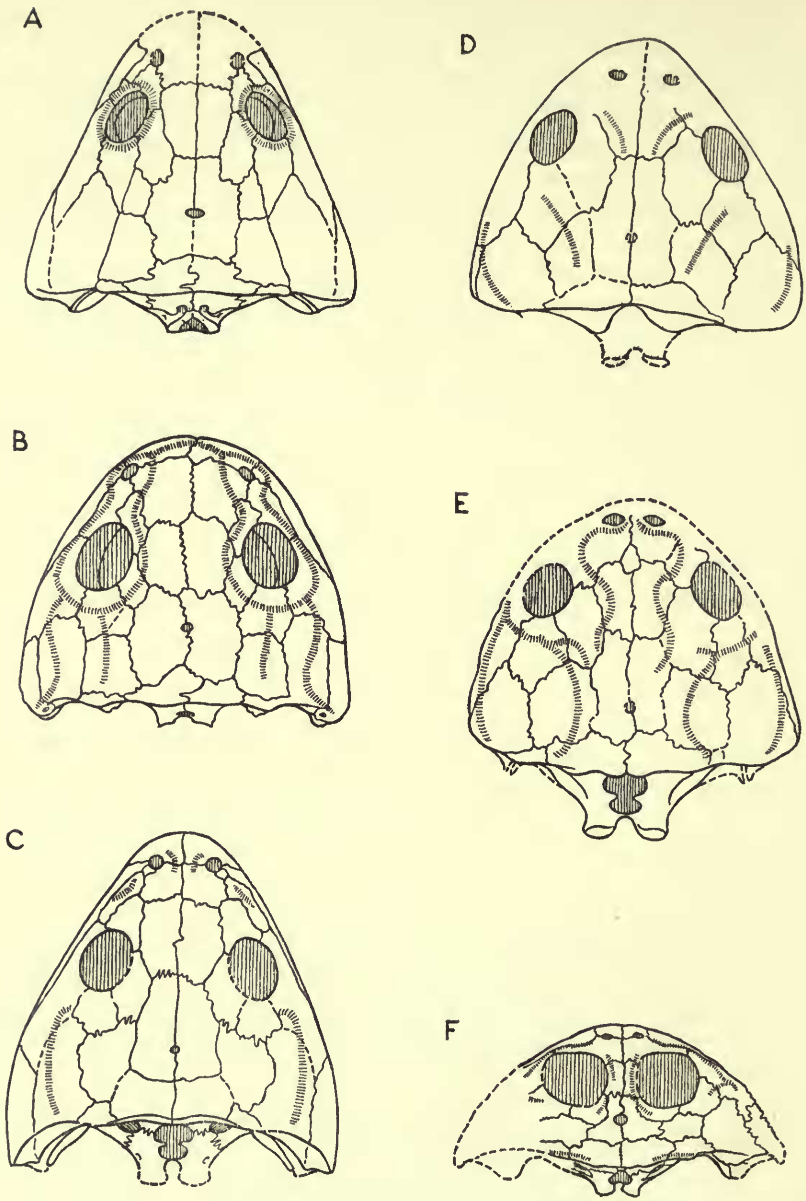
(6) The occipital aspect of the skull of *Eobrachyops* shows a deep occiput and very ventrally placed quadrate condyles. *Bothriceps*, *Batrachosuchus* and *Gerrothorax* show a progressive flattening, both of the lateral suspensory parts of the skull and of the occiput.

(7) The quadrate, which in *Eobrachyops* is on the level of the occipital condyle when the skull is viewed laterally, moves forward in late forms like *Batrachosuchus* and *Gerrothorax*.

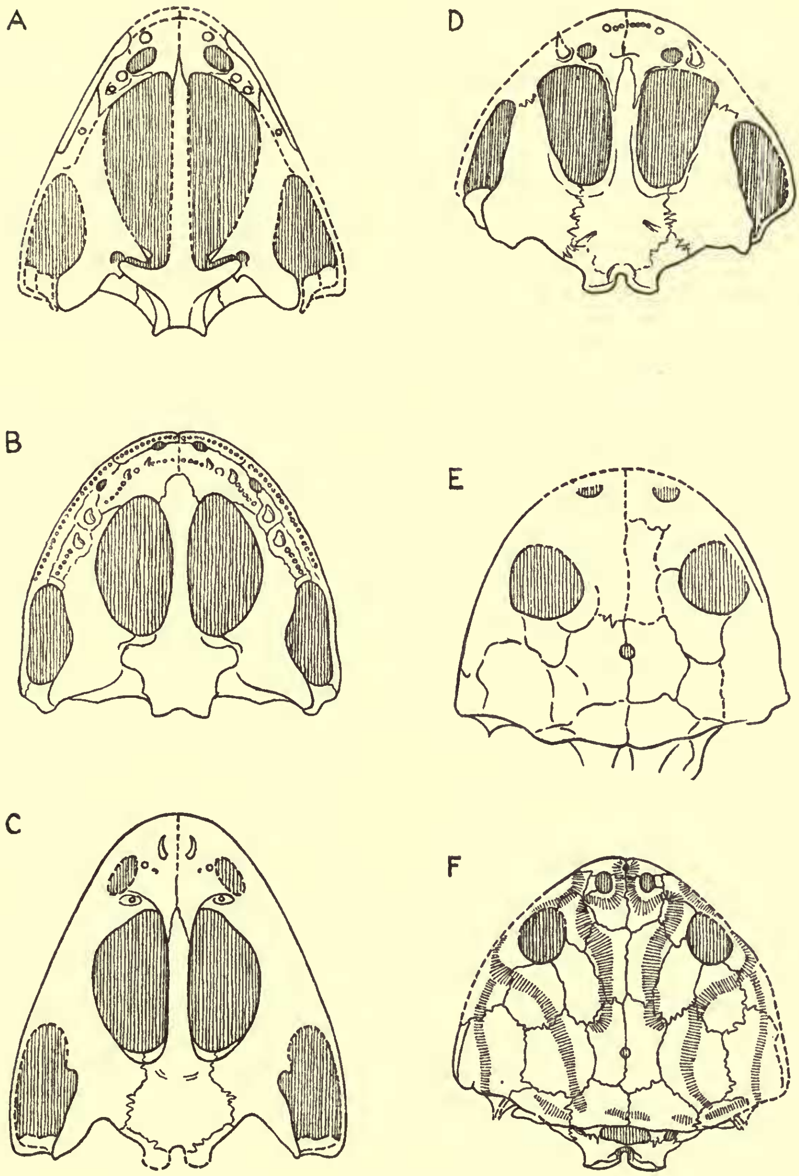
(8) The interpterygoid vacuities of *Eobrachyops* are of very great size, and there is no real possibility of their increase in later members of the group.

(9) The retroarticular process of the lower jaw, present in *Eobrachyops*, considerable in *Bothriceps*, becomes large in *Batrachosuchus* and immense in *Plagiosuchus*.

(10) The intertemporal, present as an independent bone in *Eobrachyops*, fuses with the postorbital in *Dvinosaurus* and vanishes in *Batrachosuchus* and all later forms,



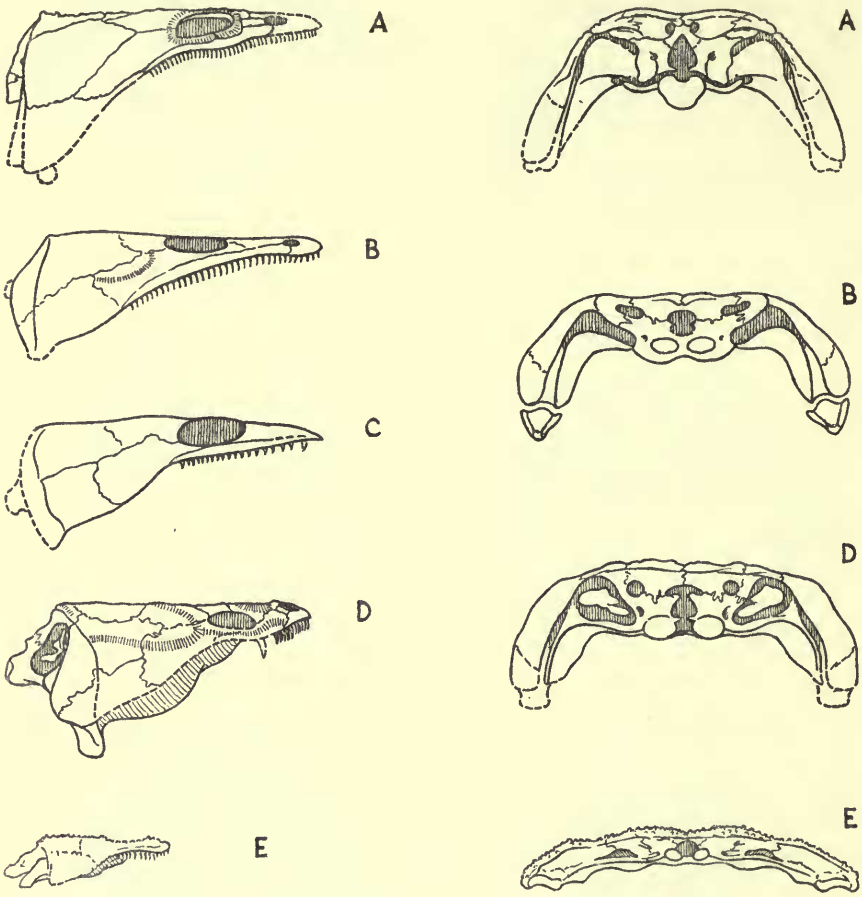
TEXT-FIG. 32.—A series of Brachyopid skulls reduced to the same width. Various magnifications. Dorsal aspects of A, *Eobrachyops townendae*, L. Permian; B, *Dvinosaurus*, U. Permian; C, *Bothriceps australis*, ? M. Permian; D, *Brachyops*, Permo-Triassic boundary; E, *Batrachosuchus browni*, L. Trias; F, *Gerrothorax pulcherrimus*, U. Trias.



TEXT-FIG. 33.—A series of Brachyopid skulls reduced to the same width, various magnifications. Palatal views of A, *Eobrachyops townendae*; B, *Dvinosaurus*; C, *Bothriceps*; D, *Batrachosuchus watsoni*. E–F, Dorsal views of E, "*Platyceps*" *wilkinsoni*; F, *Batrachosuchus watsoni*.

the supratemporal thus coming into contact with the postfrontal, as in rhachitomous and stereospondylous Labyrinthodonts in general.

(11) *Eobrachyops* has protorhachitomous vertebrae, in *Dvinosaurus* they are rhachitomous, though the first vertebra lacks a pleurocentrum, and that of the next



TEXT-FIG. 34.—A series of Brachyopid skulls reduced to the same width, various magnifications. Left-hand column lateral aspects, right-hand column occipital views. A, *Eobrachyops townendae*; B, *Bothriceps australis*; C, *Brachyops*; D, *Batrachosuchus watsoni*; E, *Gerrothorax pulcherrimus*.

two fuses with the intercentrum and neural arch. In Plagiosaurs the neural arch and intercentrum alone remain, the latter bone taking on the appearance of a centrum.

Thus in all important matters the course of evolutionary change in Brachyopids is uniform in direction over the immensely long history of the group, and is the same fundamentally as that found in the Capitosaur relatives.

This paper was begun during the war years, carried further in the late 1940's and

finally written in University College in 1954. All the drawings, which are reconstructions based on careful measurements made from adequate materials, were made by Miss J. Townend after detailed discussions, extending over very long periods, of the significance of all visible details, and the text owes much to her suggestions.

I am indebted to the Royal Society for enabling Miss Townend to work with me, and to University College, London, and Professor Medawar for their hospitality to Miss Townend and myself. The departmental staff deserve our thanks, and we owe much to the splendid photographs made by Mr. W. H. Brackenbury on which our restorations are often based.

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EXPLANATION OF PLATE 39

"*Platyceps*" *wilkinsoni* Stephens, type specimen. × 3. Narrabeen beds, Gosford, New South Wales. Property of the N.S.W. Geological Survey, Sydney, Australia. (Compare outline Text-fig. 11.)